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PHYSICAL-CHEMICAL VARIABLES IN A MINNESOTA LAKE

HENRY J. OOSTING

THE INFLUENCE OF CLIMATIC AND WEATHER FACTORS UPON THE NUMBER OF BIRDS UPON A DEPOSITING CREEK BANK

JESSE M. SHAVER

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BY

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Duke University

CONTRIBUTION FROM THE DEPARTMENT OF BOTANY
UNIVERSITY OF MINNESOTA

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PHYSICAL-CHEMICAL VARIABLES IN A MINNESOTA LAKE

I. INTRODUCTION

Much work has been done on the physical and chemical variables in aquatic habitats by Birge and Juday, the pioneers in this country, Wedderburn and his associates in England, Wesenburg-Lund, Thieneman and Naumann in continental Europe, and many others. However, information is not yet complete. A knowledge of the relationships of these variables to each other and to the organisms present is important for the interpretation of the conditions occurring in the apparently simple but actually complex aquatic habitat. Such studies then, are of interest to the pure scientist and have their application in fish culture and the preservation of wild game. Being primarily interested in aquatic flowering plants, our efforts were directed toward them, although much of the information obtained is applicable to the other forms of life present.

The particular object of this study was the extension of the type of work done in Wisconsin by Birge and Juday and their students to the region of the upper Mississippi Valley. The plan, in outline, was to make as complete a hydrographic survey as possible of the lake under consideration; to make detailed studies of the physical-chemical variables in the water and substratum; to study the distribution and succession of the higher plants; and finally, to determine, if possible, the mutual relationships between the vegetation and the above mentioned variables. Ham Lake was chosen for the study because it is a typical representative of a large number of essentially similar lakes lying in the Anoka sand plain.

The first studies of physical-chemical conditions in a lake should provide general information as to the character of that lake in comparison with others and what its general conditions are during the course of the year. To this end, the first summer's work was devoted to obtaining the ordinary hydrographic data such as soundings, mapping, etc. Also, physical-chemical studies were made of depth series samples taken near the center of the lake and always at approximately the same position. This same type of preliminary work was done on Snail Lake a few miles distant.

Knowing that depth-series data on temperature, dissolved gases, etc., as determined in 1928 are a fair indication of what conditions will be in other years (see references of Birge, Birge and Juday, Bronsted and Wesenburg-Lund, Scott, Thienemann, Clemens, Wedderburn) this phase of the work was not continued in 1929. Instead all efforts were directed toward a study of the horizontal variation of these same variables at different stations characterized by contrasting vegetation types. The irregularity of the results led

to observations of these same stations through periods of twenty-four hours.

My thanks are due to various members of the Department of Botany, University of Minnesota and particularly to Dr. W. S. Cooper for advice and assistance. Much of the field and laboratory work was possible only through the aid of Minor M. White and Mrs. Oosting.

II. GEOLOGY AND VEGETATION OF THE SAND PLAIN

Ham Lake lies in the township of the same name, in the center of Anoka County, Minnesota, and is about twenty miles north of Minneapolis.

It is one of a number of lakes of similar origin occupying pits in a great sandy outwash plain covering an area of eight hundred square miles north-east of the Mississippi River between St. Cloud and Minneapolis. This plain is flat in general, with a very gentle gradient from north-west to south-east. It is surrounded by till of Early and Late Wisconsin age, and isolated areas of the same are found within it. Parts of it are almost featureless, other parts moderately rolling, the maximum local relief being about forty feet. Lakes of various sizes are numerous, occupying the larger depressions which, as a rule, have rather abrupt marginal slopes.

The history of the plain as presented by Cooper (1933), is briefly as follows. During late Wisconsin time an extrusion of ice from the Keewatin center (the Des Moines Lobe) moved down the Red River valley and the present course of the Minnesota River, reaching its final limit near Des Moines, Iowa. A peculiar thumb-like projection from this mass (the Grantsburg Sublobe) extended northeastward, pushing the Mississippi River before it so that it came to flow along the northern margin of the ice. The Grantsburg Sublobe, probably a transitory affair, shrank very rapidly. During this process the Mississippi, an enormous glacial river heavily loaded with sediment, followed the receding ice margin step by step, flowing over large areas of stagnant ice and burying them under the load of sand which it carried. Thus there developed, over a large part of the area formerly occupied by the Grantsburg Sublobe, a great sheet of water-borne sand, flat for the most part, but rolling and with pits of various sizes where the melting of buried ice masses brought about the slumping of the superjacent materials. Ham Lake owes its origin to these processes.

The sand plain just described is covered for the most part by a forest of oaks in which *Quercus ellipsoidalis* E. J. Hill is decidedly the dominant species. Other trees occurring frequently are *Quercus macrocarpa* Michx., *Q. alba* L., *Beutla papyrifera* Marsh. and *Populus tremuloides* Michx. In a few localities there are relict colonies of northern species, *Pinus strobus* L., *P. banksiana* Lamb. and very rarely *P. resinosa* Ait. With these are found certain herbaceous species commonly associated with them in their general northern range.

The coarser soil phases are characterized by prairie vegetation in which the bunch-grasses *Andropogon furcatus* Muhl., *A. scoparius* Michx., *Koeleria cristata* (L.) Pers., *Stipa spartea* Trin., *Panicum virgatum* L., *Bouteloua hirsuta* Lag. and *B. curtipendula* (Michx.) Torr. are dominant. *Quercus macrocarpa* frequently grows in scattered fashion with these grasses, producing oak savannah of varying degrees of density. A very similar vegetation is found upon certain areas where the surface has been blown into dunes.

In the depressions, hydrarch succession of the usual type takes place. The lakes are filling much more through the agency of vegetation than by ordinary sedimentation. The shallow depressions, even those of considerable size, have reached a stage where the peat, accumulated through the activity of previous stages, has become covered with a uniform carpet of sedges and grasses among which *Carex oligosperma* Michx, is all-important. The bog-forest stage has been attained in many localities, *Larix laricina* (Du Roi) Koch. being universally present in such places and *Picea mariana* (Mill.) BSP. in a few. It is only in the larger lakes, of which Ham Lake is a typical example, that we find the earlier stages of the hydrarch succession still present.

III. HYDROGRAPHY OF HAM LAKE

Ham Lake was at one time of considerably greater size than at present and is just now gradually shrinking as is true of many of the glacial lakes in Minnesota. The general hydrographic features are given in Table I.

The shore line, which is somewhat over two miles long, varies considerably from place to place. The shrinking of the lake has left wide expanses of sandy beach and again, where the water has receded from the shallow depressions of the basin, the margins are extremely boggy.

No detailed maps of the region are available, consequently it was necessary to make a rough survey of the lake. This was done in 1929 with a plane table and an open-sight alidade. The resulting map proved fairly satisfactory. However, in 1930, Dr. W. S. Cooper, incidentally to other aerial work in progress, was able to obtain excellent vertical aerial photographs of the lake. These, when matched and enlarged gave a base map from which tracings for field work could be made in a few moments and to which the bottom contours were later added.

All depths were determined by soundings taken from a boat at intervals of fifteen oarstrokes in parallel crossings of the lake. The rowing was invariably done by the same person to insure the greatest possible uniformity. The spacing of the soundings show some irregularity due to the use of different boats and to wind-drift, but the cross lines check so closely that the depths as shown are considered as accurate as necessary.

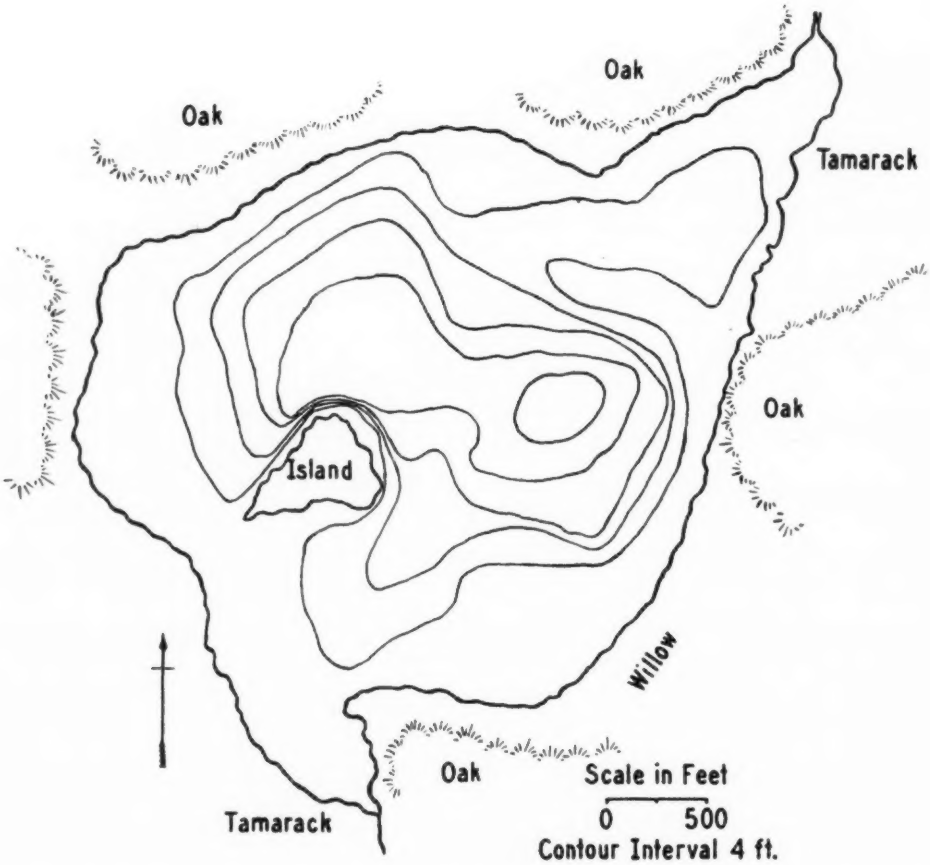

FIG. 1. Outline map of Ham Lake with bottom contours shown at 4-foot intervals.

TABLE I. *Hydrographic Data.*

Elevation	900 ft.	Shore development	1.1764
Greatest length	.9 mi.	Volume	48,590,000 cu. ft.
		% Volume of strata	
Greatest breadth	.6 mi.	To. 4 ft.	43.9%
		8 ft.	25.1
Length of shore-line	2 mi.	12 ft.	16.4
		16 ft.	10.6
Area	159.4 acres	20 ft.	3.8
		20 ft.	0.4
Island	4.2 acres	No. of soundings	239
Depth	max. 23.5 ft. / mean 7.0 ft.	Date	1928-1930

The altitude is as given by Upham (1888).

The surface areas and the planes of the contour levels were obtained by means of a planimeter used on tracings from the aerial map with contours inserted. The volumes as here given are derived from the application of Penck's formula (Penck 1894).

$$V = \frac{h(s_1 + s_2 + \sqrt{s_1 s_2})}{3} \quad \text{in which}$$

s_1 and s_2 are the areas of the planes bounding the strata and h the contour interval of 4 feet. The total volume then is the sum of all strata. The mean depth is equal to V/area. The four foot contour interval was used because four feet is the approximate limit of emergent vegetation and 8 feet the limit of submerged vegetation.

"Shore development" (Juday 1914) is the ratio of actual length of shore line to the circumference of a circle with area equal to that of a lake. Since the simplest ratio is unity, the nearer the ratio is to one, the simpler the shoreline and the more nearly it approaches a circle.

The contour map and profiles show few striking irregularities in the bottom topography, most of these having been obliterated or reduced by filling. The deepest part of the lake (23.5 ft.) is approximately in the center of the present open water.

In general the bottom slopes rather gradually toward the deepest portion. An exception is the sharp drop from the north and east shores of the island.

Although the soils of the area surrounding the lake are all sandy, there is very little sandy bottom. Only where shallow marginal terraces occur, for example along the east shore of the island, and where the bottom has a gentle slope exposed to wave action, as on the east and southeast shore, is there any clean, sandy bottom. The latter type occurs in a strip extending from the south along the east shore and then swings out into a bar or spit across the northeast arm.

Borings in the peat and marl deposits show that the substratum is everywhere sand, even where twenty feet of filling has taken place. No attempt was made to ascertain the thickness of the sand underlying the lake.

Aside from the sandy areas just described the bottom is uniformly composed of organic materials and marl and silt in various proportions and different degrees of aggradation. The north shore proper has been built up the least but is everywhere floored by a layer of silty marl and fine plant remains which varies from a few inches to several feet in thickness. The northeast arm is nowhere more than five feet deep and, where the vegetation is most profuse, somewhat less. There is here an accumulation of plant material resulting from years of decay, and quantities of almost pure marl, all of which rests on the original sand bottom ten or fifteen feet below the surface. Along the west shore and in the south-west bayou accumulation has probably been even greater, for the emergent vegetation ending at the four foot depth-contour, is superposed upon twenty feet of accumulated material. Here, again, the samples brought up from beyond the first few feet are almost pure marl, the plant remains and sand particles being negligible in quantity. The filling materials in Ham Lake agree with those observed in Anoka County by Roth (1917). He found most of the deposits resting upon sand although the soil maps indicate clay. Marl was found to be the predominant filling agent and organic materials were in most cases well decomposed. In deeper water the bottom is covered to a depth of a foot or more with a silty ooze, including decayed planktonic forms, fragments of the higher plants and some marl.

Because there is very little run-off from the rather level and very previous sand plain and consequently little erosion, and because the single inlet is practically blocked, the amount of mineral soil being carried into the lake and deposited there is very slight. Most of the filling would seem to be directly due to the activities of the organisms present in the water.

Old shore lines, still plainly marked, show that at one time the water surface was five feet or more above the present level. The mean level has apparently fallen steadily and the decline is still in progress. Each succeeding summer of observation has shown a further lowering, with the minimum for 1930 at least a foot below that of 1929. Farmers living near the lake say they have never seen it as low as in 1930, but that within their period of observation the level has fluctuated several feet.

Other nearby lakes have a comparable history. Laddie Lake, eight and one-half miles south of Ham Lake, was practically dry in the fall of 1927 and during the years 1928-29. However, during this driest of summers, 1930, it practically maintained its early spring level, and much of the emergent vegetation, principally cat-tails, died out, so that it appeared once more as a lake. Moore Lake, four miles farther south, has experienced similar changes. Bunker Lake, three and one-half miles southwest of Ham Lake, has had a recent history similar to that of the latter, having steadily shrunken until in the fall of 1930 there was practically no open water left. According to near by inhabitants, however, this lake has undergone pronounced fluctuations while it has been under observation. In 1888, 1904, and 1913 it was full to the brim; in the intervals between these dates it reached low levels comparable with the present.

The general statement may safely be made that the water table of the sand plain, and therefore the lake levels, fluctuates in a periodic manner, which is doubtless to be correlated in general with fluctuations in precipitation. There is, however, lack of uniformity in response among the lakes, and we frequently find cases where water level seems almost independent of precipitation curve and drainage. The fluctuation of lake levels remains an unsolved and inviting problem. As to Ham Lake, its history for the last few years has been one of fluctuation, with an extreme minimum in 1930. Whether this latest phase represents a true progressive decline cannot at present be determined.

There are no streams flowing into the lake at present. A small stream must have flowed into the north arm long after the bog had become established. I have observed no water entering at this point, although the old channel has only a heavy floating mat over it as yet. There is no evidence of springs. At the south end of the lake a small outlet creek, in the spring, trickles through a rather wide, irregular, boggy channel that connects with several tamarack bogs to the south and west which were formerly parts of the lake. In summer, it is practically choked with vegetation.

IV. PHYSICAL-CHEMICAL STUDIES

LIGHT; TRANSPARENCY

In the study of light intensity at various depths, the photochemical reaction of potassium iodide and sulphuric acid was used. In this reaction hydriodic acid is oxidized and iodine released. The rate of decomposition in light is proportional to the light intensity (Plotnikoff 1907). McCrea (1923) summarizes the possibilities and limitations of the method and his suggestions for obtaining the best results were followed. The concentrations of solutions here used were those suggested by Pearsall (1917).

The apparatus consisted of a series of uniform test tubes attached to strong cords which held them in a horizontal position. The whole was held submerged by a weight at the lower end, adjustable so that a large flat cork at the opposite end floated just at the surface of the water. On this cork was a wire clip for holding the first test tube fully exposed to the light. The other tubes which were attached to the cords at two foot intervals were held at two, four, six and eight feet from the surface.

Since the mixture of the two reagents (KI and H_2SO_4) is unstable even in the dark, the solutions were kept separate and then placed in the test tubes in the field immediately preceding their use. Ten cc. of each solution were used in each test tube. At the same time a check for normal deterioration was prepared and kept in the dark. The titration of the check was done at the same time as the regular solutions and the data as here expressed have been corrected accordingly.

TABLE 2. *Light Intensities.*

1929

	Aug. 8 (1-5 P.M.)	Aug. 17 (12-5 P.M.	Aug. 22 (12-4:30 P.M.)	Aug. 27 (10:30-4 P.M.)
Surface	100%	100%	100%	100%
2 ft.	13.5	5.49	4.39	20.38
4 ft.	9.8	0.5	0.0	2.42
6 ft.	3.9	0.5	0.0	0.48
8 ft.	0.0	0.0	0.0	0.0
Transparency	3 ft.	2 ft. 4 in.	2 ft. 2 in.	3 ft.

1930

	Aug. 5 (10:30-4:30)	Aug. 16 (11-4)	Sept. 1 (12-5)	Sept. 7 (11:30-5:30)
Surface	100%	100%	100%	100%
2 ft.	49.02	13.85	9.72	5.6
4 ft.	22.55	3.08	2.16	1.12
6 ft.	.98	1.54	1.31	1.12
8 ft.	0.0	0.0	0.0	0.0
Transparency	3 ft. 3 in.	2 ft. 9 in.	2 ft. 6 in.	2 ft. 3 in.

Transparencies 1928

Ham Lake		Snail Lake	
July	15—4 ft. 3 in.	Aug.	11—7 ft. 9 in.
	21—4 ft.		18—7 ft. 10 in.
	28—3 ft. 6 in.		25—8 ft. 6 in.
Aug.	14—3 ft.		
	31—3 ft. 9 in.		

The amount of thiosulphate required to titrate the surface solution was taken as standard or 100% Light Intensity (L.I.) and the titrations of the samples at the various depths, expressed as percentages of the standard, represent the per cent Light Intensity at these depths.

The eight foot limit for determinations was used, since this is the depth limit for flowering plants in Ham Lake.

If the solutions are exposed for an extended period (Braid 1923) the iodine liberated produces first a pale yellow color which gradually darkens to brown and finally to deep sherry. The deeply colored solution will absorb many of the active rays and reduce the effective action of some of the rays of the spectrum. Also, the increase in concentration of the free iodine will proportionately cut down the rate of dissociation. Both of these limitations were found by Braid to be true when exposures of twenty-four hours or more were made.

In this work these limitations would not seem to apply. All the determinations were made between the hours of 10 a.m. and 5 p.m. and, even with the strongest light, this is too short a time for the action to be retarded. Even the solution exposed to full sunlight at the surface rarely approached the deep sherry, and the submerged solutions scarcely passed the pale straw color. Since the period was short and since the color of the solutions was never of the deepest, it is not probable that the concentration of liberated iodine had reached the point where it materially reduced the rate of dissociation.

For determining the relative amount of light absorption by the various strata of water in a lake, this method appears entirely satisfactory. If it were being used as a basis for measuring the total amount of light, at a given point, for an extended period of time, its value might well be questioned.

Determinations of the transparency of the water were made by the use of a Secchi disk (10 cm. in diameter and plain white). The data, as presented, are the averages of several determinations of the depth at which such a disk disappeared when lowered into the water in full sunlight and close to noon.

The amount of light available to plants at different depths was of interest. The Light Intensity Curves (Fig. 2) have the usual and expected form (Birge 1913; Pearsall 1917; Pietenpol 1918) i.e., rapid falling off in the surface layers followed by a tendency to flatten out abruptly. Judging by the results of others, the absorption in the surface layers is greater than would have been expected. In all but one instance the Light Intensity is reduced to twenty per cent in the first two feet. This is of course due to absorption by the suspended material, substances in solution and to some extent by the water itself. Plankton, living and dead, is abundant in Ham Lake all through the summer. Suspended silty material is always apparent. The color of the water

is consequently rather brownish. This color is in all probability due largely to the materials in suspension and solution derived from the bogs at the ends of the lake.

Because of selective absorption by materials in solution and suspension and also by the water itself the light measured at different depths could not have been of the same quality.

However that may be, light in Ham Lake certainly becomes a limiting factor at relatively slight depths. Pearsall (1920) found that a Light Intensity of two per cent was the limit of growth for flowering plants in the English lakes studied. He also found that this two per cent Light Intensity was definitely related to the transparency as determined by a Secchi disk, his conclusion being that the depth of two per cent Light Intensity might be considered as one meter *above* the depth at which the disk disappeared. This made it possible to use the simple Secchi disk method for determining the limit of the "photic" zone.

Pearsall's conclusions are not applicable to Ham Lake. During 1929 the determinations of Light Intensity show the two per cent limit to be one foot

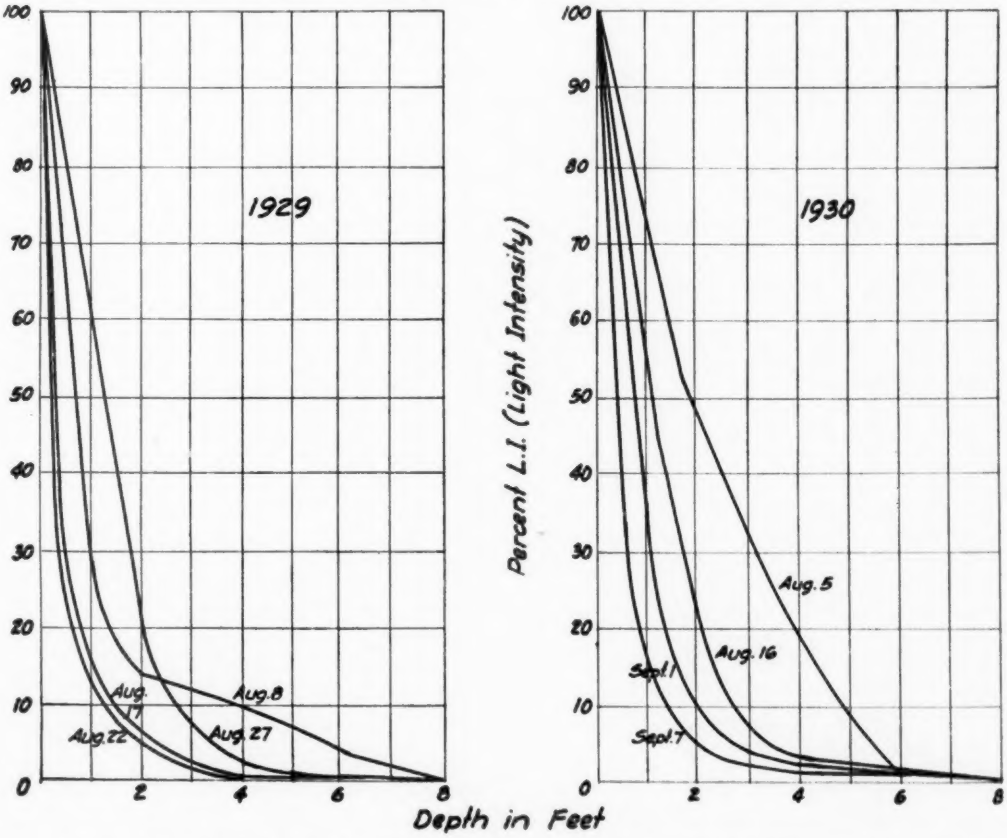

FIG. 2. Light intensity at different depths in Ham Lake during the summers of 1929 and 1930. The intensity measured at each depth is expressd in per cent of the surface intensity.

below the level of disappearance of the disk on three occasions and three feet *below* on a fourth. Through the summer of 1930 the two per cent Light Intensity limit was approximately two and one-half feet *below* the level of disappearance of the disk. Rickett (1922; 1924) in his work on Green Lake

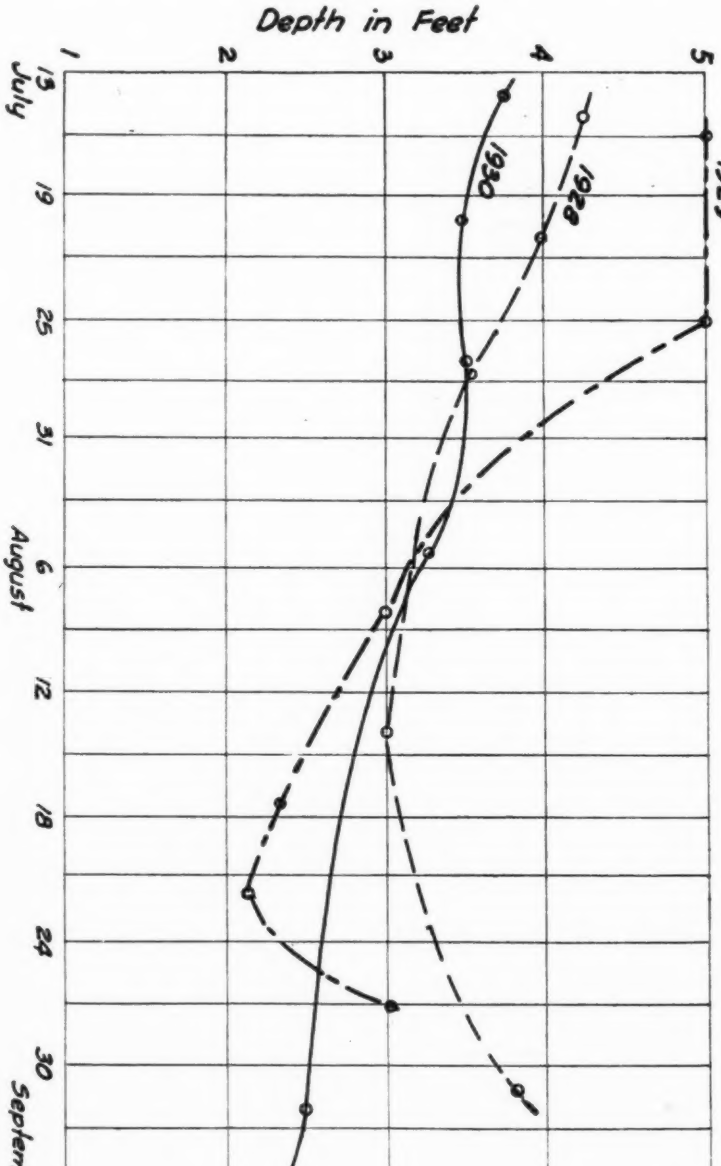

FIG. 3. Comparison of transparencies of Ham Lake water for the years 1928-29-30 as measured with a Secchi disk. The depth at which the disk disappeared when lowered into the water is recorded in feet.

and Lake Mendota in Wisconsin, found the vegetation limit to conform more closely to the one per cent Light Intensity limit. Conditions in Ham Lake seem to be in agreement with Rickett's observations. During midsummer,

with average water level, the vegetation limit is between seven and eight feet and the Light Intensity at this depth is reduced to one per cent or even less.

The average light intensities for the various depths studies are as follows:

	2 ft.	4 ft.	6 ft.	8 ft.
1929	10.94%	3.18%	1.23%	0
1930	19.54%	7.22%	1.24%	0

Here the two per cent average Light Intensity is well above six feet, probably somewhere between five and six feet, for both 1929 and 1930. These averages would also make it appear that light absorption in the upper strata was greater during 1929 than 1930.

In Figure 3 the changes in transparency for the three summers of study are shown as curves. The greatest transparency was always in mid-July with a decrease through the summer. In 1928 and 1929 there was an increase in late August but in 1930 the decrease continued into September. This progressive decrease in transparency through the summer with the increase in the fall is probably correlated with the total plankton present. Although the algal plankton is selective in absorption, the colorless forms, alive, or dead and slowly settling out, all combine to increase the turbidity, which results in increase of the total absorption and reduction in transparency. The work of West and West (1912) is an example of what has been done on plankton periodicity. Their curves for phytoplankton occurrence are not parallel for all species but they do, in a general way, follow the curve of temperature. An abrupt decrease in temperature causes the plankton total to fall off immediately and the gradual increase of temperatures through the summer produces an increasing plankton count if other conditions are equal. It would be expected, then, that the curve of transparency would descend progressively through the summer and ascend again in late summer as the water cleared when plankton decreased. The continued decrease of transparency in September, 1930 is probably due to the high temperatures which continued well into the month.

Temperature

All temperatures were taken with a Centigrade thermometer inserted in the rubber stopper of one of the water sampling bottles described later. The bulb was pushed well down in the bottle, but enough of the thermometer projected to permit reading without removing the stopper. By bringing the samples to the surface quickly and making the reading at once, there was little chance for the temperature to change. For the depths employed, this arrangement was found very satisfactory.

Depth series temperatures are shown in Figure 4 which illustrates the gradual warming of such a lake as the season progresses. Since operations were transferred to Snail Lake during the month of August, we can only

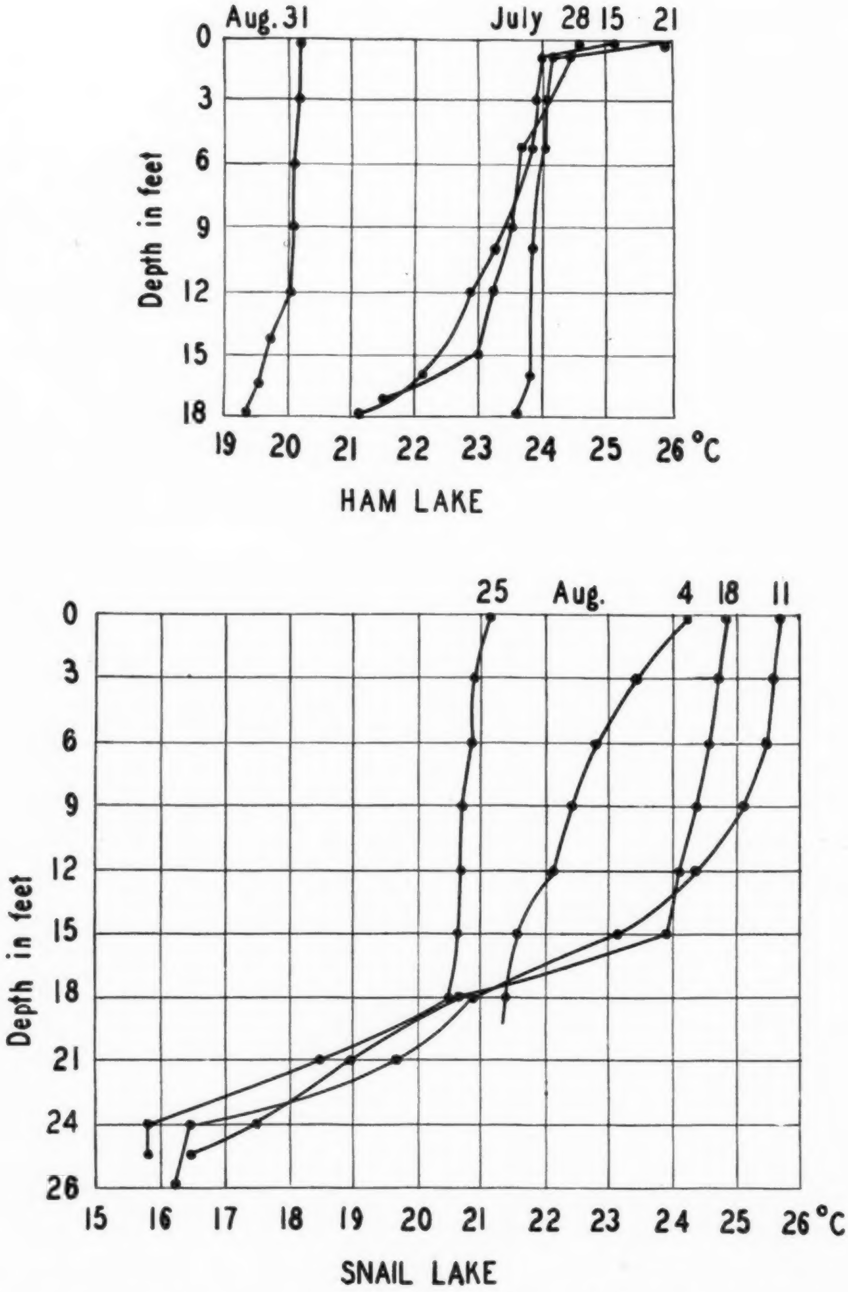

FIG. 4. Depth series temperatures for Ham and Snail Lakes in 1928.

judge from conditions there what must have occurred at Ham Lake. In all comparisons between the two it must be remembered that Snail Lake is somewhat larger and, in general, several feet deeper. The temperatures appear to have increased generally until about August 11. After this date they declined through the whole lake, with the greatest decrease in the upper strata.

As a result, the depth series temperature curve for August 31 approaches a straight line, for the difference between the temperature of the surface and bottom strata is only 0.9 degrees. These temperature curves are as might be expected in a lake with a maximum depth of twenty-three and one-half feet (Birge & Juday 1911; Scott 1916; etc.).

Mean Temperatures. Multiplying the percentage volume of each stratum by the mean temperature of that stratum and summing the products gives a reasonably accurate figure for the mean temperature of a lake. Birge & Juday (1914) say, "It is fair to conclude that the mean temperature of the water of a lake of simple form in late summer may be derived from a single series of observations taken at or near the center of oscillation." They also give data to show that such a series of temperatures may be considered as sufficient basis for the drawing of conclusions of a more general nature. From the careful and detailed studies of Birge (1903; 1910; 1913), Birge and Juday (1911; 1914), Bronsted and Wesenburg-Lund (1911), Wedderburn (1907) and others, we know, even from a series of data so brief as the present what the general temperature conditions will be in a lake throughout the year and probably for years to come. The mean temperatures of Ham Lake for certain days and for the entire summer follow.

July 15	July 21	July 28	Aug. 31	Summer
23.8	24.48	24.0	20.15	23.08

The mean temperatures in Ham Lake are high as compared to larger bodies of water of greater depth. The absence of a thermocline permits the temperature of the lower strata to increase or decrease directly as the surface waters are heated or cooled. Warm water from the surface, moved by the wind, may warm the bottom strata at any time during the summer, and cooling in the fall is appreciable at the bottom almost as soon as in the surface waters. This accounts for the difference between the mean temperature for the summer and the mean temperature for August 31. The entire lake from top to bottom had already been affected by a few cooler fall nights. Consideration of the high mean temperature for July 21 in conjunction with the temperature curves shows how quickly heat is distributed to the lower strata in such shallow water. In fact, fluctuations of temperature for the different strata follow almost parallel curves throughout the summer.

The stations with one species of plant predominant *(Eleocharis, Scirpus, Nymphozanthus, Zizania, Typha, Chara, Elodea)* studied in 1929 were visited each day that field work was done. Water samples and temperatures were taken at about four o'clock to make them comparable from day to day.

It appears that temperature has little bearing on the type of vegetation present but that vegetation may have considerable effect on temperature. This is especially true in shallow water where the mass of vegetation may be so great as to restrict water movements. All the stations were in two to four

feet of water and at such depths the heavy vegetation is particularly effective. The *Elodea* station in two and one-half feet of water had the highest temperatures (29° to 33° C.). The *Elodea* itself grew so luxuriantly as to make it almost impossible to force a boat through it, and the station was protected from wave action by a zone of *Scirpus* and *Nymphozanthus*. The *Chara* station showed the temperatures resulting from lack of protective vegetation in open shallow water (two and one-half feet). The *Chara* grew profusely but only on the bottom and interfered but slightly with wave action or currents. As a consequence the temperatures there were the most erratic of all the stations and did not follow the general trend.

The remaining five stations had strikingly uniform temperature changes, the greatest range on any day being 3° C. The irregularities were mostly due to the direction and strength of the wind. The lowest temperature (24.2° C.) was found at the *Scirpus* station on August 8; the highest (30.5° C.) at the *Typha* station on July 25.

In Ham Lake the widest range of temperature from top to bottom was 4.1 degrees, while the difference between surface and ten or twelve feet was rarely more than two degrees and the vegetation limit is eight feet. In Snail Lake the difference between surface and fifteen feet did not exceed 2.5 degrees; nevertheless the vegetation ceases at twelve feet. It is probable that such slight temperature variation is not sufficient to determine vegetation limits. This is in agreement with Pearsall (1920). He found that nearly uniform temperatures extend to depths beyond the photic zone in his lakes and therefore disagrees with the theory of Magnin (1893) that temperature limits the depth of vegetation. He further states that the only effect temperature has on lake vegetation is in limiting the growing season, because of the time required to warm a lake in the spring. This is especially evident when comparison is made with pond vegetation. *Sagittaria latifolia* Willd. illustrates this difference. In shallow ponds in this section it flowers approximately one month before it does in the lakes. The truly active growing season in Minnesota lakes is restricted to the months of July and August.

This limiting of the growing season is probably related, to some extent, to the temperature of the bottom mud. Pearsall (1920) holds that lake muds have temperatures like the waters which bathe them. Birge, Juday and March (1927) show this to be true, in general, except that there is a lag change of bottom temperature as compared with change in water temperature. In the spring this lag would delay germination, and renewal of growth from rhizomes would be retarded.

OXYGEN

Methods. The Winkler method of oxygen determination was used throughout this work. Concentrations of solutions were such that the final

titration in cc. was equal to parts per million of dissolved oxygen (Theriault 1925). The titrations were usually made in the field, soon after the samples were taken. Occasionally this was not practicable and the samples were brought in to the laboratory, but the reagents necessary for titration were always added in the field.

All water samples were collected in 250 cc. bottles with ground glass stoppers. Because all the samples were from comparatively shallow water the sampler was a simple device. The bottles were clamped in pairs to a short rod weighted at the lower end. Each bottle was fitted with a two-holed rubber stopper with a long and short glass tube. By having one tube reaching the bottom of the bottle, and one just through the stopper, the bottle would fill from the bottom without bubbling and without disturbing the water at the level of sampling. For depth sampling a rubber cap was slipped over one of the tubes on each bottle. At the desired depth these could be freed by means of a string leading to the surface.

The percentage saturations are taken from the tabulation in "Standard Methods of Water Analysis" (1925) as calculated in milligrams per liter by Whipple and Whipple (1911) and Fox's determinations (1909) of the solubility of oxygen in distilled water. Barometer readings are made at the Minneapolis meteorological station every even hour and in making corrections for barometric pressure the reading nearest preceding the time of collection was used. No attempt was made to correct for humidity.

Vertical Oxygen Variation 1928. The depth series determinations made at intervals during the summer are shown in Figure 5 expressed as parts per million.

The general decrease in oxygen concentration with increase in depth is commonly explained as due to the dead plankton settling out and decomposing. In Ham Lake, the most abrupt decrease was near the bottom. No oxygen was present at fifteen feet July 21, and July 28 shows only 1.05 cc. per liter at fourteen feet. The uniform oxygen concentrations of August 31 may be due to mixing by the wind, made possible by the decrease in temperature and consequent reduction in resistance to mixing.

Snail Lake appears to have a thermocline region so near the bottom that only a few feet of water represent the hypolimnion. It is possible that the lake has, very locally, a greater depth than twenty-six feet but no soundings showed more. On August 11 and 18, what appears to be a thermocline was present between fifteen and twenty-four feet, while, on August 25, it had lowered and become limited to the water between eighteen and twenty-four feet.

Through this stratum of water the curves of temperature and oxygen parallel each other. The decrease of oxygen in the thermocline is considered as being due to the decaying plankton settling from the epilimnion and

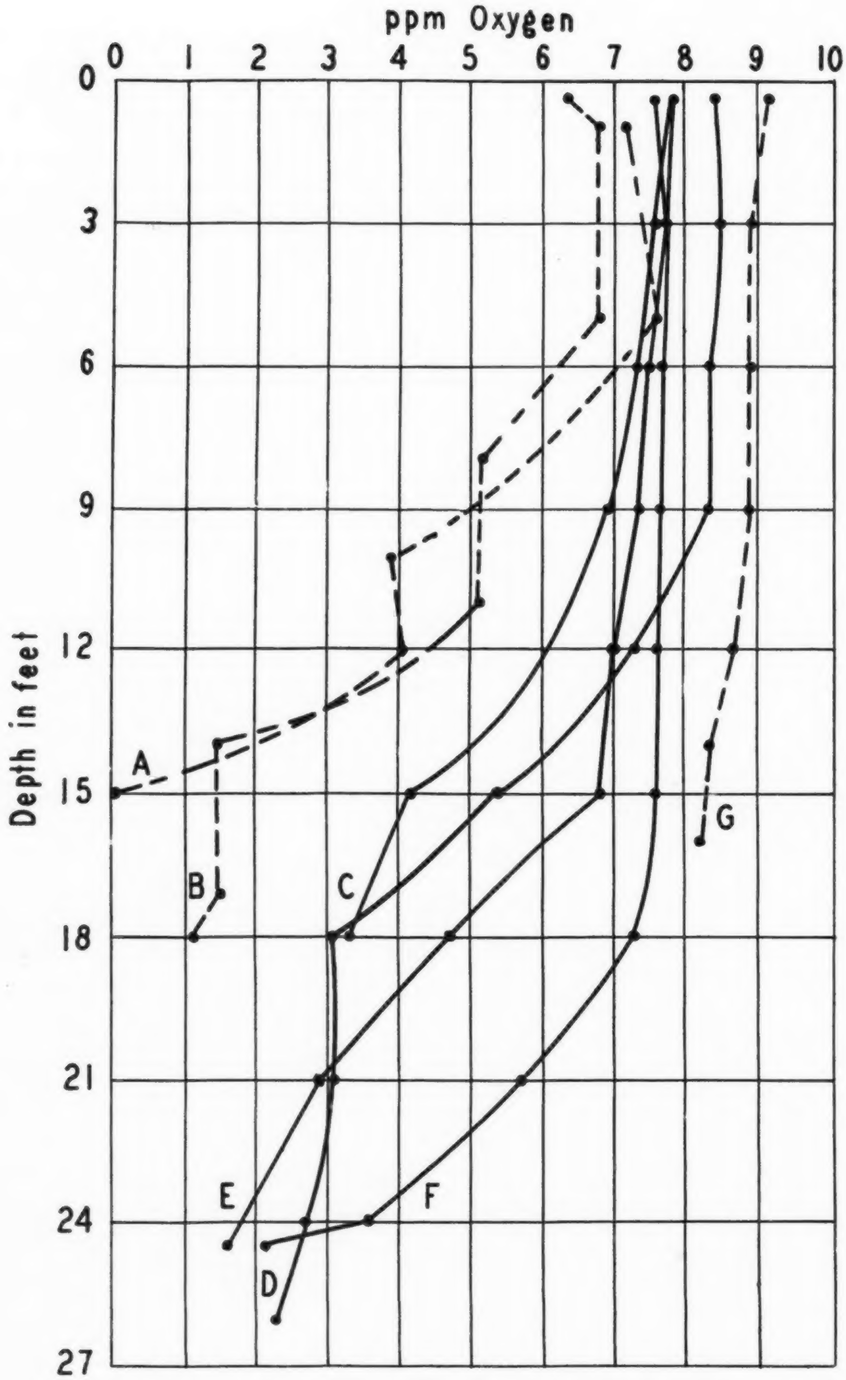

FIG. 5. Depth series oxygen concentrations for Ham (- - -) and Snail (——) Lakes, 1928. A, July 21; B, July 28; C, August 4; D, August 11; E, August 18; F, August 25; G, August 31.

being concentrated in the thermocline because of the greater density of the water. Whether or not this stratum is considered as a thermocline the reason for the decrease would be the same and to be expected. The smooth fit of the oxygen and temperature curves is striking.

Scattered collections from shallow water with contrasting vegetation showed striking differences in dissolved oxygen concentration including many values that were excessively high. These samples were taken with no regularity and with no definite plan in mind so their results are of no value, except to show the advisability of making a systematic study of oxygen changes in different habitats.

Horizontal Oxygen Variation 1929. Collections were made at the contrasting stations described under Temperature each day in the field, in the late afternoon when the maximum effect of photosynthesis would be apparent in oxygen concentration. Samples were taken at about one and a half foot depths. The lowering of the water level ruined the *Elodea* station in August, and the *Potamogeton compressus* station, which was in a rather exposed position, had begun to disintegrate before the end of July.

Changes in wind, temperature, etc. appear to affect various stations differently. Consequently, there is very little consistency in the results (Fig. 6). There is a wide variation between stations on a given day, and the factors concerned are too complex to permit explanation of the fluctuations from week to week. *Chara* and *Elodea* stations were consistently high in dissolved oxygen, while the *Nymphozanthus* station was low. The peak of dissolved oxygen concentration for all stations seems to be in early August when photosynthetic activity is high. All except *Chara* fell off in late August as would be expected.

The northwest arm, being very shallow, with a long gradual sloping bottom, is choked with vegetation, which is densest where the water is two feet deep and which thins out gradually, until at five feet there is practically open water. During 1929, water samples were taken along a line running from a point where vegetation was so dense that a boat could not be pushed through to open water. In the shallow water there was an almost pure stand of *Zizania*, which changed rather sharply to submerged vegetation, heavily massed and made up mostly of *Potamogeton compressus* and *Ceratophyllum* with a few patches of yellow water lilies. Farther out, the water lilies disappeared and the two former species became dominant. As the water increased in depth the vegetation thinned out to scattered clumps at four feet and at five feet practically open water was reached.

In this series the highest dissolved oxygen in early July was in open water (11.3 ppm; 150%) while the lowest was in the *Zizania* (7.8 ppm; 95%). The *Zizania* maintained approximately this concentration through the summer. Through July the highest saturation appeared in the lily-pad

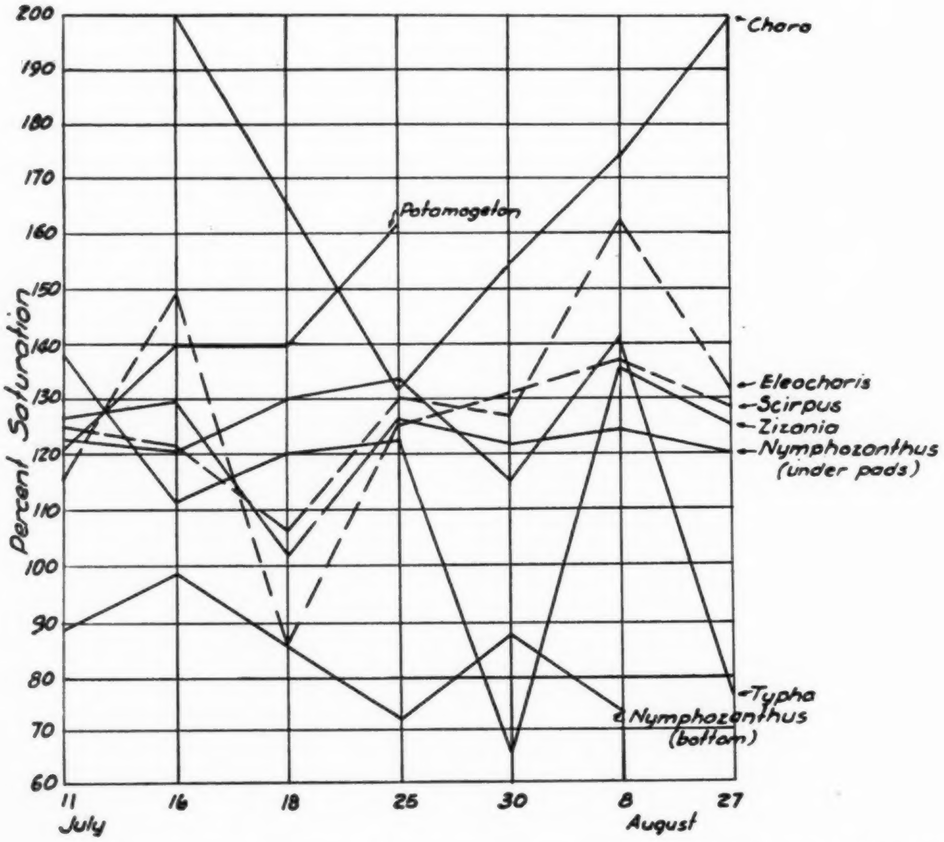

FIG. 6. Oxygen variation at different vegetation stations in Ham Lake, 1929. The changes for a station throughout the summer are shown horizontally; differences between stations at a given hour on a particular day, vertically.

and submerged girdle (15 ppm; 200-210%) with a gradual decrease outward to open water (7-8 ppm; 95-105%). During August there appeared a tendency for all points in the series to equalize, for the extreme range of saturations was reduced to only twenty-five per cent.

The extreme range in concentration is striking. On July 25, the difference was 125% of saturation (8.3 ppm), and the two samples were collected not more than fifteen yards apart. On July 18, these two points had a difference of 114% (8.4 ppm), while on August 31 it was only 25% (1.9 ppm), showing a tendency toward uniformity, even open water being within this range and approaching the highest dissolved oxygen.

The striking variability in dissolved oxygen in a short space may be further illustrated. On July 18, the highest dissolved oxygen (15.5 ppm; 204.8%) was found just under the lily pads. At a depth of about two feet at this same point (next to the muddy bottom) the dissolved oxygen was only 15.9% (1.3 ppm), a difference of 189%. On July 25, the difference at this

same point was 182%. Other points along the line have a similar variation, although not so extreme.

Open shallow water is of course more uniform. On July 25, in practically open water, the one and one-half foot sample showed 95.9%, while at a depth of four and one-half feet (bottom) there was 102% dissolved oxygen.

The difference between surface and bottom in the heavily massed vegetation, is explainable. The large amount of massed photosynthetic surface, activated by high temperature, was giving off oxygen rapidly. Thus, high concentrations were produced in spite of the falling off of solubility with high temperature. At the same time in such massed material there would be much decaying matter at the bottom. As a matter of fact, this vegetation is underlain by fifteen to twenty feet of peat and marl. It is not impossible that oxidation of these plant remains would take up oxygen faster than it could diffuse from the photosynthetic region above. At the same time, the respiration of living plant parts and of the myriad animal forms living in such stagnant warm water, would consume a considerable amount of the dissolved oxygen available.

CARBON DIOXIDE

Relationships and Methods. Carbon dioxide relationships in lake water have been studied and clearly stated by several authors (Birge and Juday 1911, 1914; Juday 1915; Kemmerer et al 1923; Scott 1916). Consequently only a brief summary is included here.

Carbon dioxide is readily soluble in water and may occur free as dissolved carbon dioxide, but is generally found in chemical union with other substances, mostly with calcium and magnesium as a normal carbonate. When free carbon dioxide and normal carbonate are present together the carbonate is converted by the carbon dioxide to bicarbonate. Much of the bicarbonate carbon dioxide fortunately remains available for photosynthesis. Since the amount of gas in solution is dependent upon its partial pressure in the atmosphere, the free carbon dioxide in water is always limited in amount and thus the carbon dioxide available in the bicarbonate becomes highly important biologically. The amount of carbonate present, then, determines how much "free" and bicarbonate carbon dioxide can be held in a lake and consequently the potential life productivity of the lake since all aquatic life is dependent on photosynthetic activity and this, in turn, on available carbon dioxide.

The Seyler method, with modifications in technique, as suggested in "Standard Methods of Water Analysis" (1925), was used in making the determinations. The results are all given in cc. of carbon dioxide per liter. The carbonates and bicarbonates are presented as "bound" and "half-bound,"

conforming with the usage in limnological work in the past. It should be remembered that "half-bound" carbon dioxide is equal to one-half the bicarbonate, and "bound" carbon dioxide includes both the carbonate carbon dioxide and one-half the bicarbonate.

Vertical Variation. During the summer of 1928, Ham Lake showed no free carbon dioxide present to a depth of sixteen feet, and no further data were collected.

The change of free carbon dioxide content in Snail Lake during the month of August, 1928, is of interest. In the early part of the month all strata had some of the gas present in small amounts, as is always true in early summer in a lake with a complete spring overturn. The amount present was least near the surface and increased gradually with depth (Table 3). One week later there was no free carbon dioxide down to fifteen feet but the amount below had increased considerably. By August 18 the highest stratum containing the gas was at eighteen feet, with only 0.5 cc. per liter. On August 25, when sampling was discontinued, there was but 0.3 cc. per liter at the eighteen foot level, and again the concentration in the lower levels had increased. It would appear that the total amount of free carbon dioxide dissolved in the lake was about constant through the month of August, and that, as the month progressed, it concentrated in the lower layers.

TABLE 3. *Carbon Dioxide: Vertical Variation 1928.* Snail Lake (cc./L).

	Aug. 4	Aug. 11	Aug. 18	Aug. 25
6 in.	.25	0	0	0
3 ft.	.51	0	0	0
6 ft.	.51	0	0	0
9 ft.	.51	0	0	0
12 ft.	.51	0	0	0
15 ft.	.51	1.0	0	0
18 ft.	.76	1.5	.51	.3
21 ft.	.76	1.8	1.00	.5
22 ft.	1.00			
24 ft.		2.0	1.80	3.0
26 ft.		2.5	2.30	3.3

Since the increase in carbon dioxide is in all cases associated with a decrease in oxygen, the changes are probably due to photosynthetic activity in the upper strata and oxidation of organic material in the lower. Photosynthesis by flowering plants and plankton in the upper strata would reduce the carbon dioxide, both "free" and "half-bound," as the summer progressed, and increase the oxygen. Plankton dying off would settle out and bits of the larger plants would descend with them. The decomposition of these materials in the lower levels would reverse the gas relations, for the oxygen would then be consumed and carbon dioxide released.

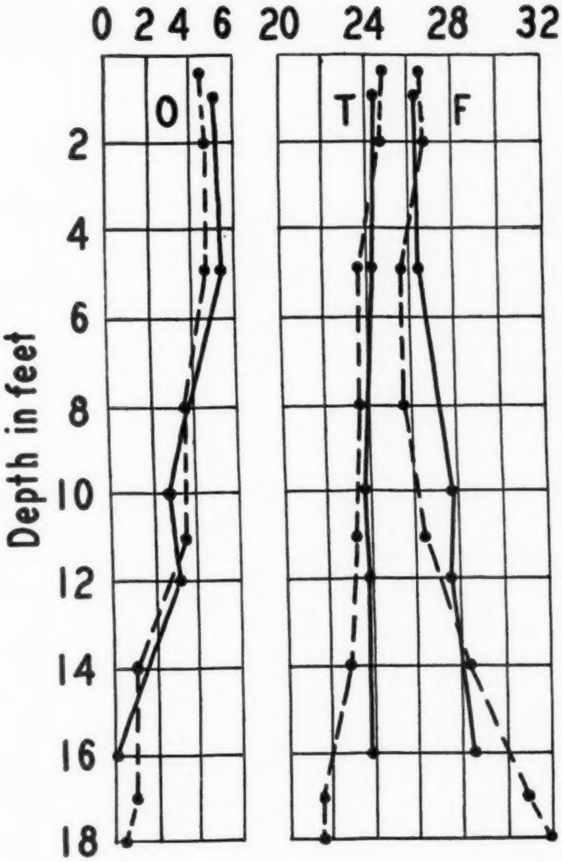

Fig. 7. Ham Lake. July 21, 1928) (——), July 28, 1928 (- - -). In Figures 7 to 12 the depth series curves for Oxygen (O), Hydrogen-Ion concentration (pH), Temperature (T), and Carbon dioxide (C) have been plotted together. The curves to the left of the zero line indicate alkalinity or the amount by which the "bound" carbon dioxide (F) exceeds the "half-bound." The same curve to the right of the zero line refers to "free" carbon dioxide. O, C and F are given in cc. per liter, T in degrees centigrade. The dots indicate the depths of sampling.

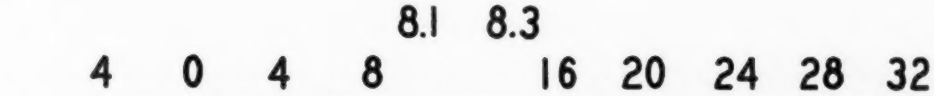

Fig. 8. Ham Lake. August 31, 1928. See Fig. 7 for explanation.

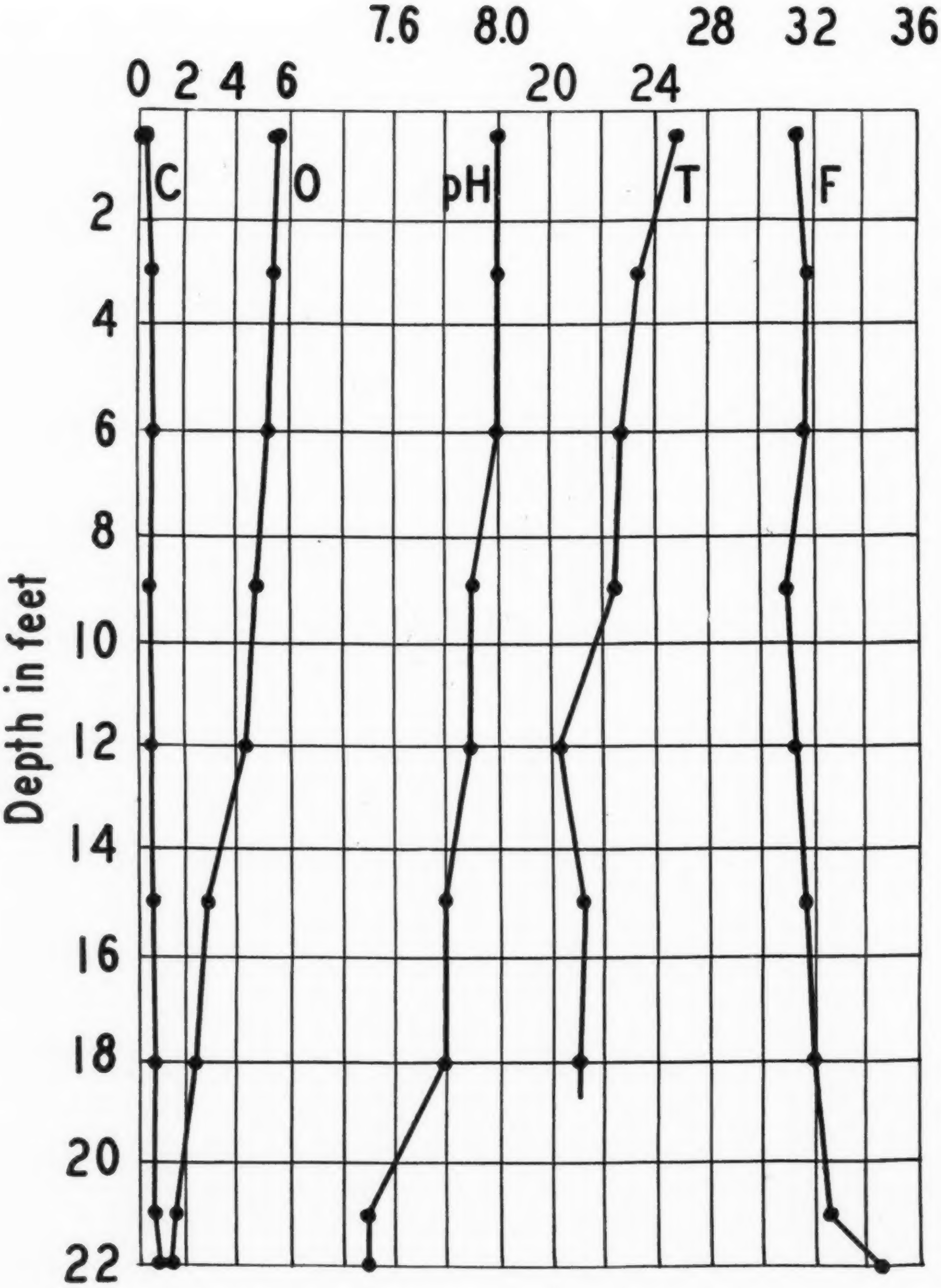

FIG. 9. Snail Lake August 4, 1928. See Fig. 7 for explanation.

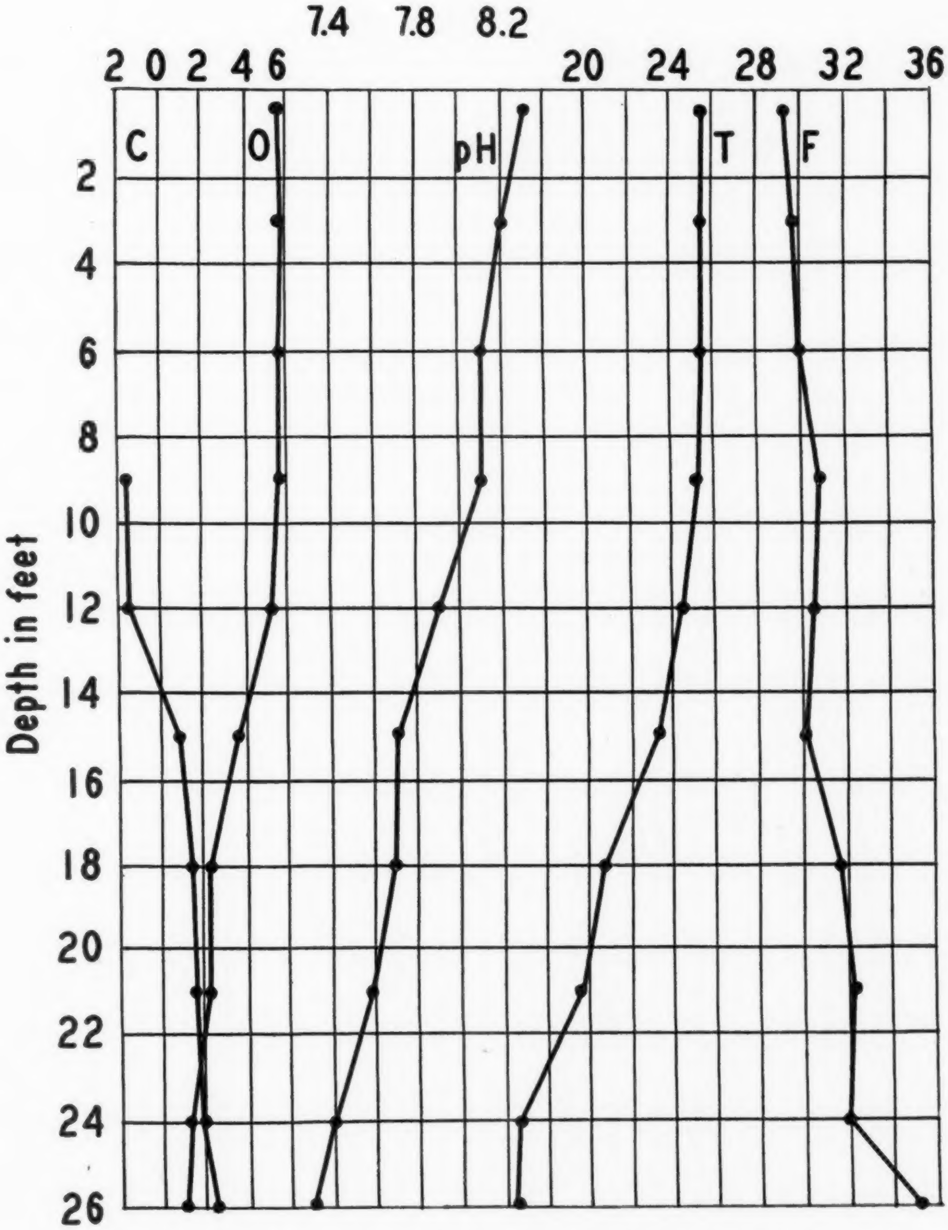

FIG. 10. Snail Lake August 11, 1928. See Fig. 7 for explanation.

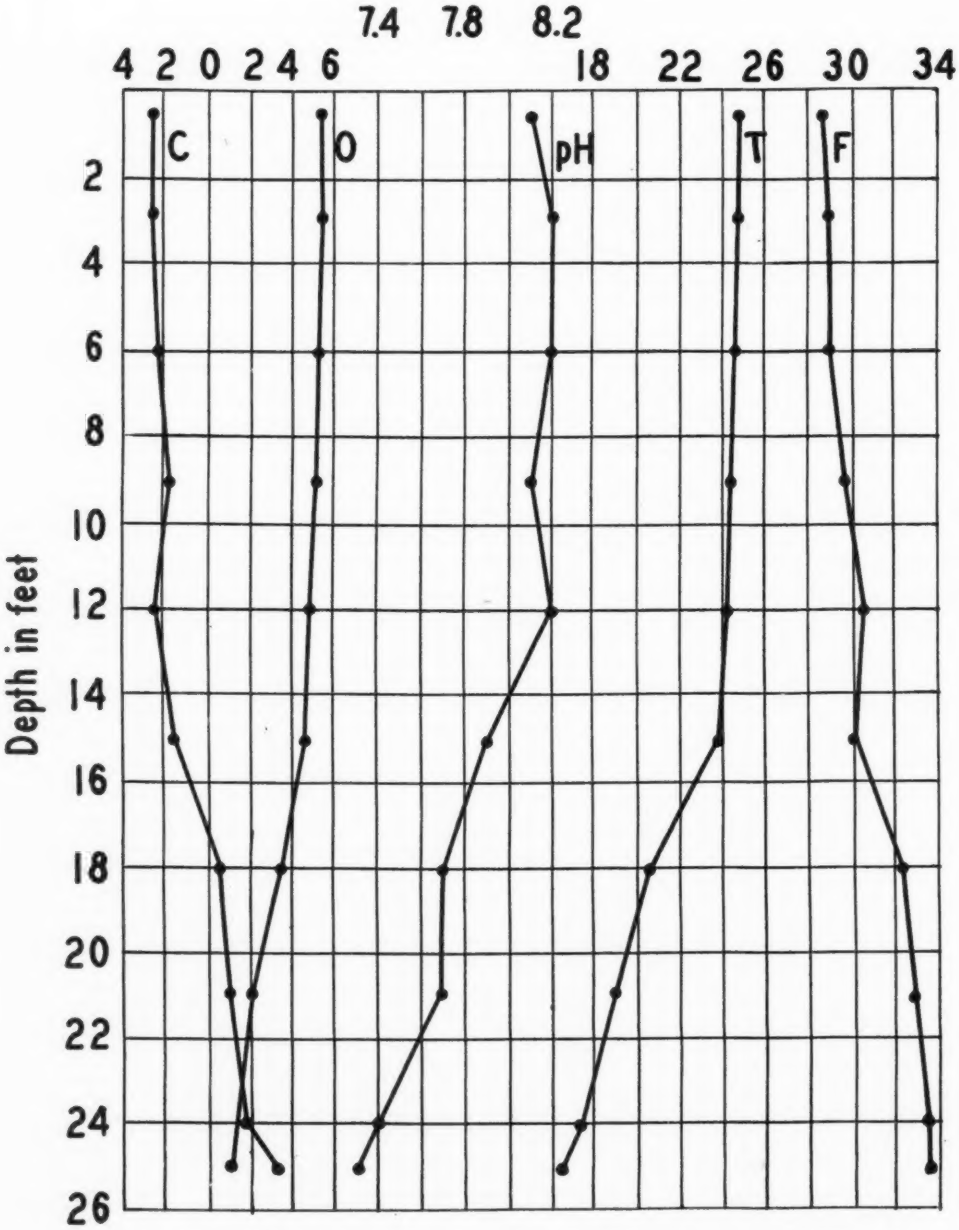

FIG. 11. Snail Lake August 18, 1928. See Fig. 7 for explanation.

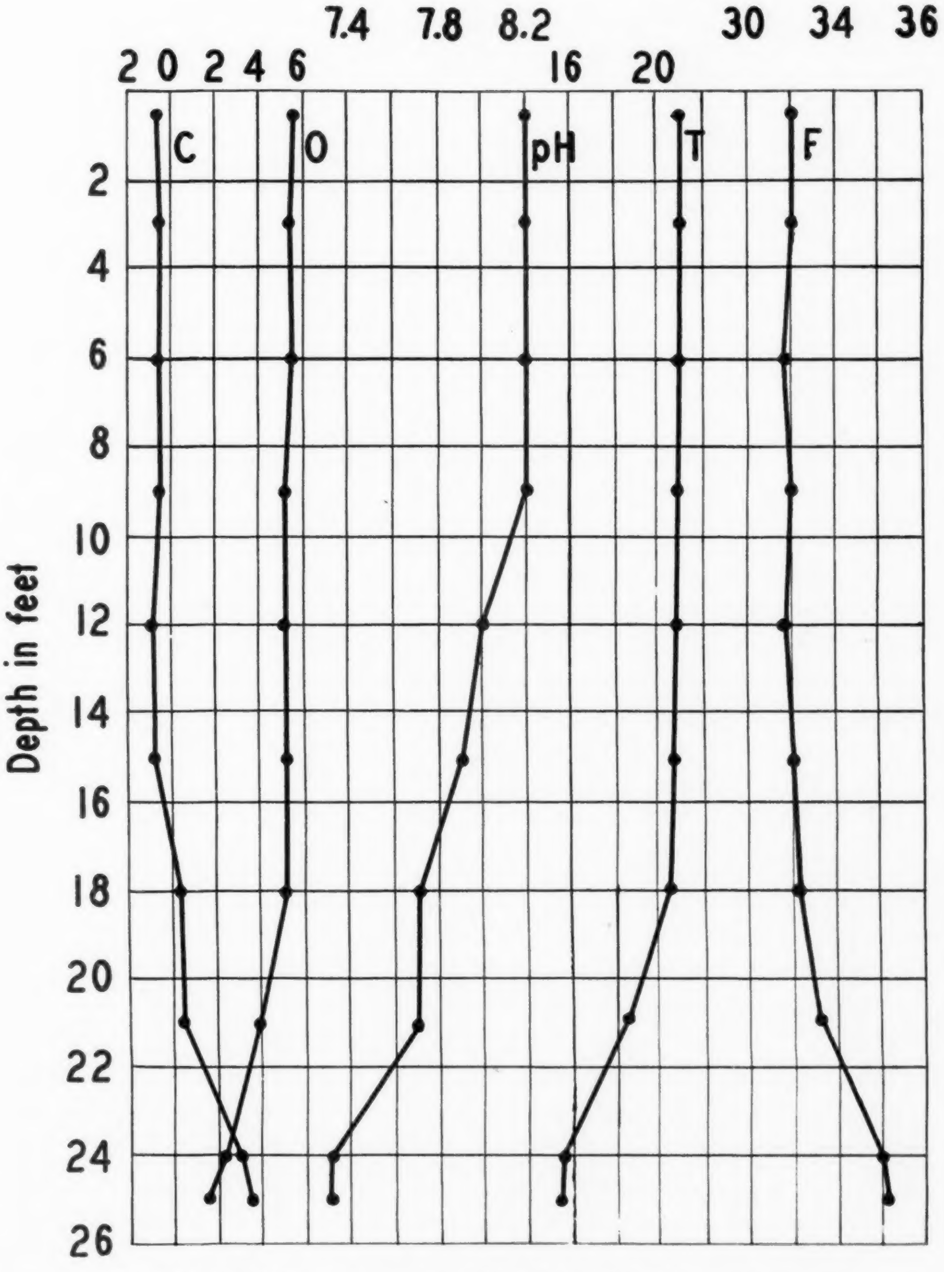

FIG. 12. Snail Lake August 25, 1928. See Fig. 7 for explanation.

Station Observations 1929. The carbon dioxide determinations made at the various stations are quite as irregular as the oxygen concentrations previously discussed. The relationship between pH and carbon dioxide, discussed later, is brought out clearly by these irregularities. Plotting the data to show the changes through the summer serves only to emphasize the extreme complexity of the relationships existing in an aquatic habitat. No broad generalizations are apparent and the changes are so irregular as to prohibit any interpretation.

HYDROGEN-ION CONCENTRATION

The hydrogen-ion concentration of water, being definitely related to the amount of carbon dioxide present (Greenfield & Baker 1920; Shelford 1923; Juday, Fred & Wilson 1924; Senior-White 1927) and being also a criterion of photosynthetic activity (Saunders 1920; Lapicque & Kergomard 1922), is always a desirable physical determination. Whenever water samples were collected, the pH was determined. The data for 1928 were obtained with a La Motte block comparator and all determinations were made in the field. During 1929, a field instrument was not available at all times and samples were brought to the laboratory for electrometric determination, using a Bailey hydrogen electrode and a type K potentiometer. In 1930, a small pocket comparator (Hellige-Klett) using colored glass standards mounted in a revolving disk was obtained for use in the field. This proved to be the most satisfactory of the apparatus used, especially because it required but a few minutes to make a determination.

Both the electrometric and colorimetric methods were checked against each other at intervals and were found to be in excellent agreement. The samples brought to the laboratory did not change in pH appreciably if carefully stoppered and if run within a few hours after collection.

Having only one depth series for 1928 in Ham Lake, we can say little as to vertical changes taking place during the season. This one does show, however, that the lake is strongly alkaline in late summer, as is true of most lakes in the region. In the data for Ham and Snail lakes, the tendency for pH to become less alkaline with increasing depth is well shown (Figs. 7-12). This of course is to be expected, for, with increasing depth, the demands on the carbon dioxide supply by photosynthesis are reduced, and decomposition near the bottom releases carbon dioxide (Juday, Fred & Wilson 1924).

The station studies of 1929 give no new information as to pH. Conditions in Ham Lake are much as those Phillip (1927) found in a similar lake not far distant. The water samples collected at the same time from different stations invariably had different hydrogen-ion concentrations ranging from pH 7.1 to 8.75 or 7.5 to 9.2 in the most extreme instances. The *Elodea* station had a uniformly high value which is not strange since there

was a great mass of vegetation actively photosynthesizing. The *Potamogeton compressus* station notably increased in bulk during July, becoming denser and more resistant to water movement around it. The result was a decrease in carbon dioxide and a corresponding increase in pH.

The water lily station shows how different the pH may be at points only a foot or two apart. This is especially well illustrated on July 25 when the surface water was highly alkaline (pH 8.9) and the bottom water two and one-half feet below was acid (pH 6.9).

The series of samples taken along the line described in the section on oxygen, from dense vegetation grading to open shallow water, consistently showed the stagnant water with the densest vegetation to be lowest in pH (about 7.3). Going outward the water became gradually more alkaline, sometimes reaching pH 9.0, and then fell off suddenly to about pH 8.0 at the beginning of open water.

TWENTY-FOUR HOUR STUDIES

The extensive observations by various students of limnology, especially Birge and Juday, have shown the seasonal and annual changes which the physical-chemical variables undergo in different types of lakes. For a lake as a whole, we have a fair idea of the general nature of the changes taking place and a reasonable expectation of what may occur under given conditions. However, our studies of these variables in Ham Lake in 1929, in contrasting vegetational stations, showed such wide horizontal variation in late afternoon and such extreme irregularities from day to day, that a more careful check of these features seemed desirable.

Most of the investigations of this type have been made with emphasis on one variable. It is, however, desirable to make simultaneous determinations of all possible factors; temperature, dissolved oxygen, hydrogen-ion concentration and carbon dioxide, because they are related to each other either directly or through the changes brought about by photosynthesizing plants, the action of plankton or decomposition of organic materials. Determinations made at short, regular intervals would serve to bring out these relationships and the degree of dependence of one variable upon another. Twenty-four hours seemed the minimum time for a satisfactory series of determinations and two-hour intervals between sampling were the minimum possible with available facilities.

On August 8 and 9, 1929, the first twenty-four-hour series was run. The same stations were used that had been studied through the summer, and at the start samples were collected from a depth of one foot and near the bottom. However, it was physically impossible to care for this number of samples and subsequently all were taken at a depth of one foot. This single series, using six stations, proved so interesting that the 24-hour sampling was

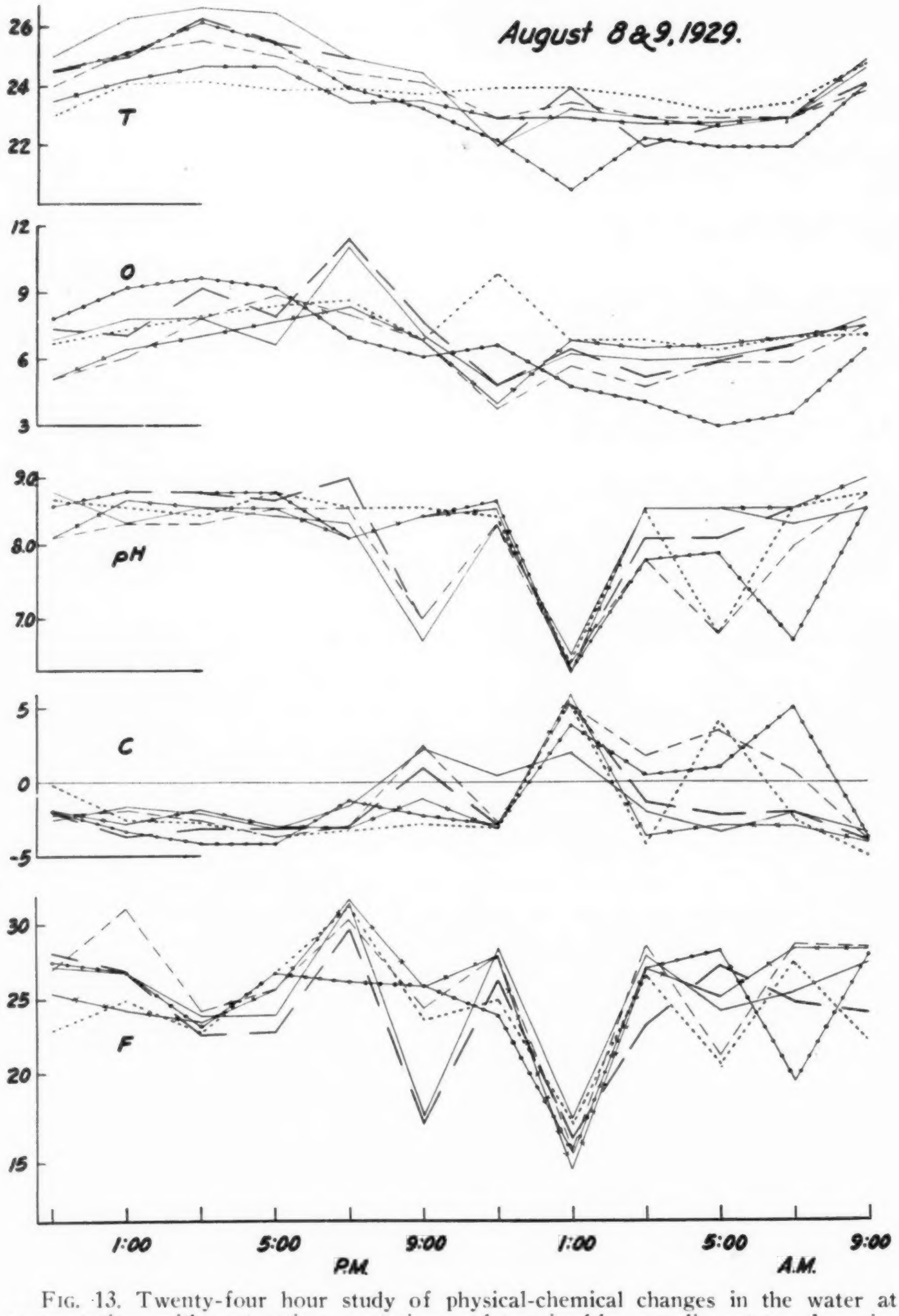

FIG. 13. Twenty-four hour study of physical-chemical changes in the water at seven stations with contrasting vegetation as determined by sampling at two hour intervals, August 8 and 9, 1929. The plan and symbols in Figures 13 to 16 are the same as in Figures 7 to 12. See Fig. 7 for explanation. The stations are represented as follows:

1930		1929
Naias	———————	Typha
Open water 1 ft.	—·—·—·—	
Open water 4 ft.	—·—·—·—·—	Chara
Equisetum	—— —— —— ——	Equisetum
Zizania	— — — — — — —	Zizania
Scirpus	. . . .	Scirpus
Nymphozanthus	—x—x—x—x—x—	Nymphozanthus

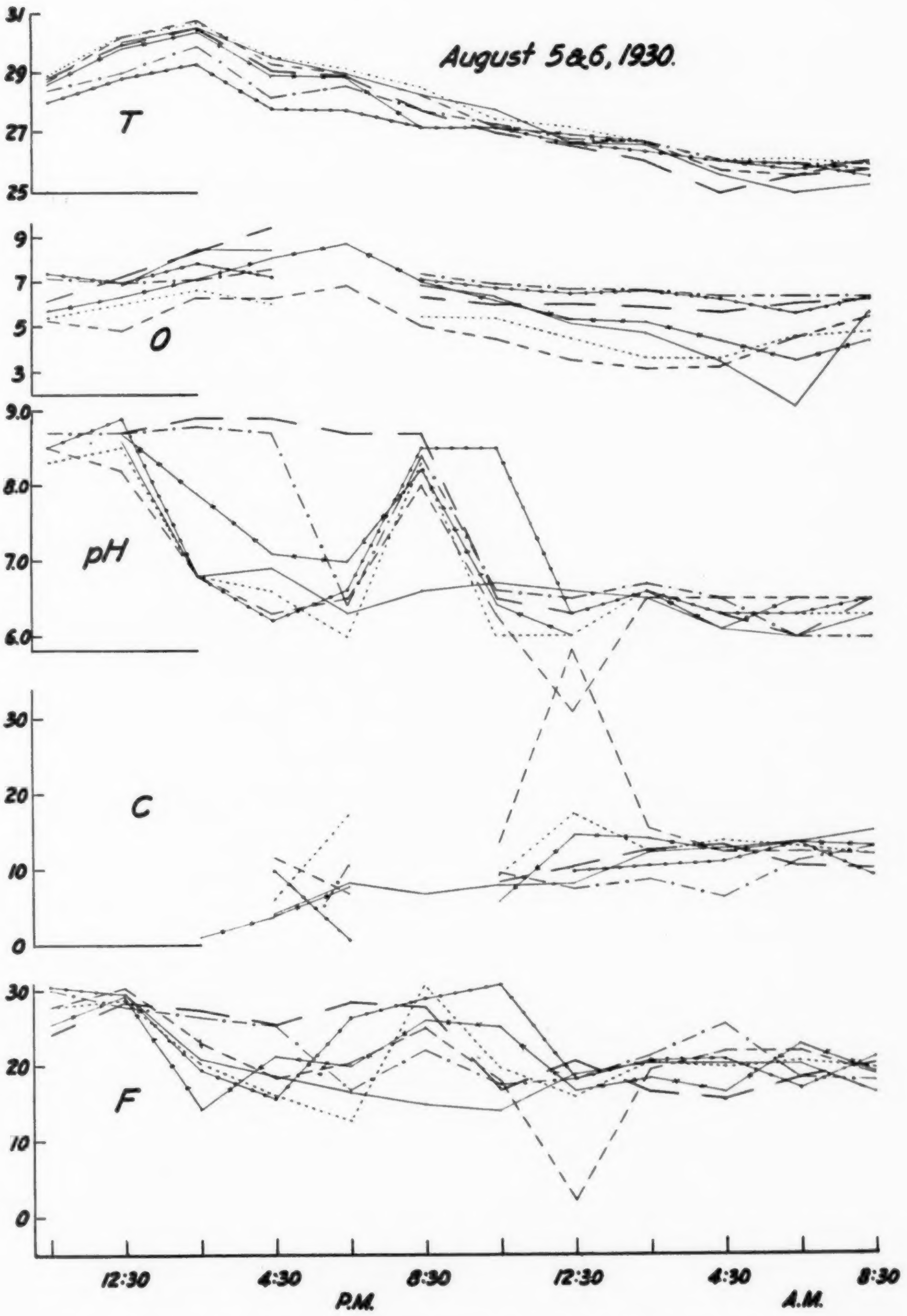

FIG. 14. Twenty-four hour study, August 5 and 6, 1930. See Fig. 13 for explanation.

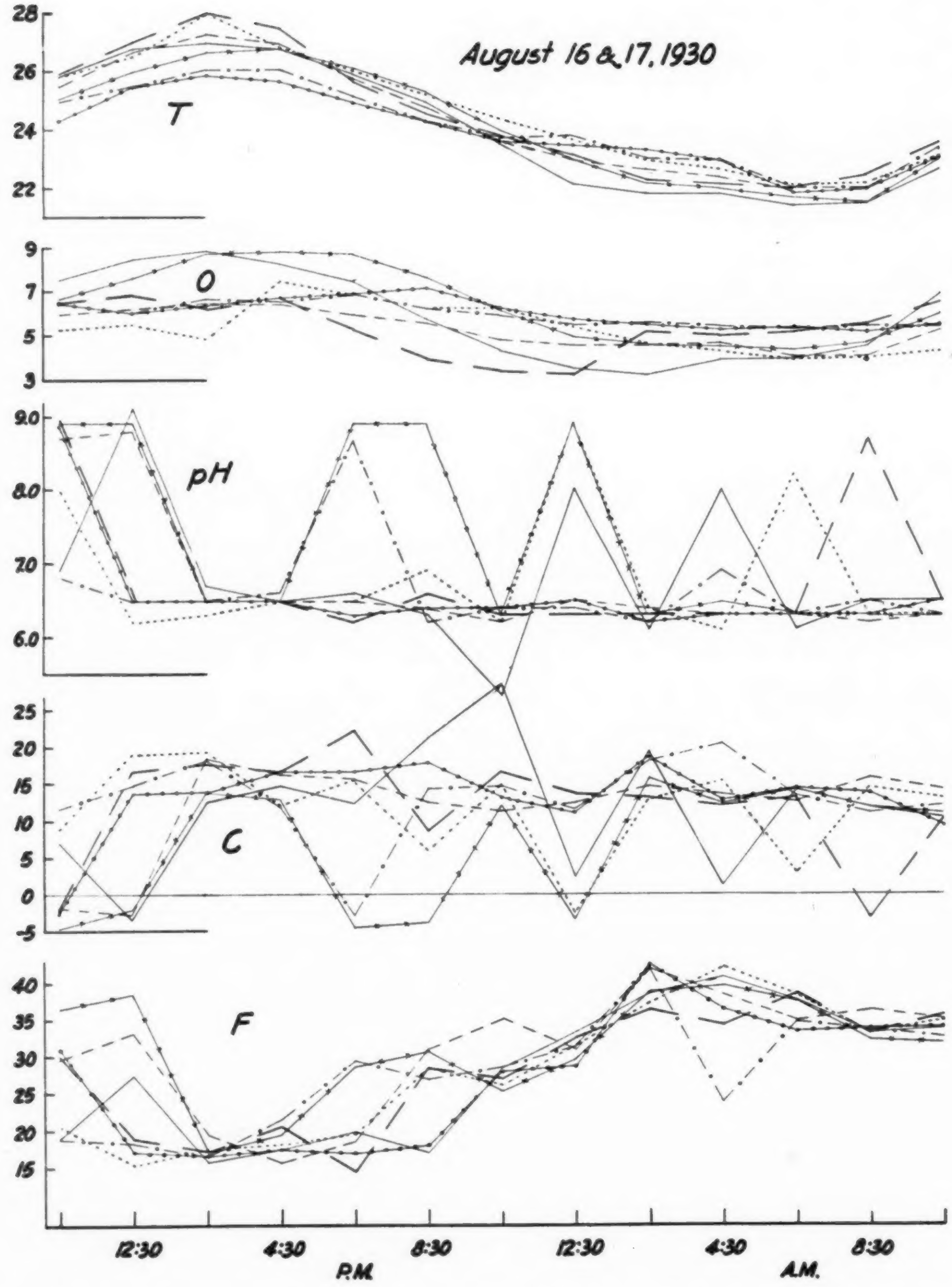

FIG. 15. Twenty-four hour study, August 16 and 17, 1930. See Fig. 13 for explanation.

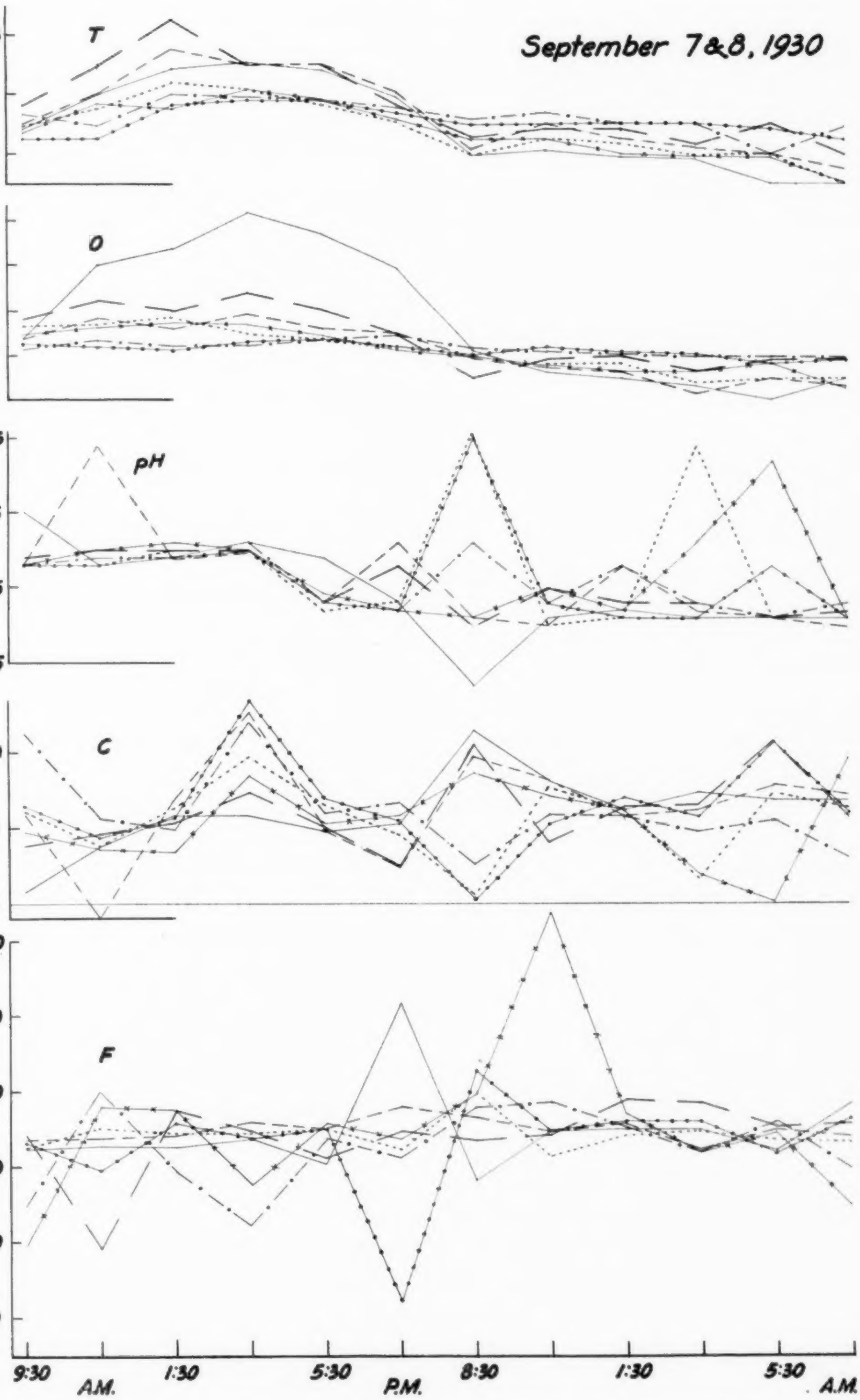

FIG. 16. Twenty-four hour study, September 7 and 8, 1930. See Fig. 13 for explanation.

continued in 1930 and series were run on August 5 and 16 and September 7. With the exception of the *Typha* station, on which observations were discontinued, the same stations were studied as in 1929. In addition, samples were taken regularly in open water at one and four foot depths. The data are presented as curves in Figures 13 to 16. The occasional breaks are at points where accidents occurred in the field.

Examination of the curves brings out certain obvious generalizations. The temperature of the water reaches a maximum at about 2:00 p.m. and then decreases to a minimum early the next morning; a rather abrupt increase follows when the effects of the sun become appreciable. Changes in the temperature of open water are much less abrupt and less extreme than those of the marginal water because of conduction from the heat-storing lower strata in the former. For the same reason the temperatures at one foot always have a slightly higher maximum and lower minimum than those at four feet.

The curves for dissolved oxygen have much the same form as those for temperature. The variation from the mean is, however, not so great and changes are not so abrupt. The greatest concentrations of oxygen are found in late afternoon when photosynthetic activity has built up the supply and just before the decreasing light and falling temperatures combine to reduce this activity.

The curves for pH and carbon dioxide are extremely irregular. The inverse relationship between free carbon dioxide and pH is, however, one of the obvious facts shown by the charts. Because each change in pH is accompanied by a proportionate but inverse change in free carbon dioxide it is probable that the pH changes are directly related to the carbon dioxide concentration. The free carbon dioxide is derived from the respiration of the organisms present and from decomposition of organic materials. While these processes are going on constantly at a varying rate, photosynthesis occurs only during daylight and the resulting carbon dioxide curves should be low during the day, increasing during the night. The pH curves should change proportionately but in the opposite direction. This general trend is apparent in two of the series but not in the others. No general explanation is possible for all of the irregularities. Undoubtedly, currents, wind and wave action play a part as causal agents. Oxygen is not affected to as great an extent because of its higher concentration in the atmosphere. The equilibrium relationship resulting from this higher partial pressure permits dissolved oxygen to be lost from the water only if its concentration is high. If the concentration is low oxygen may be taken up by the water when the surface is disturbed.

The apparently inconsistent changes in carbon dioxide and pH would seem impossible were it not that at certain hours these changes appear at all stations with almost identical decreases and increases. On August 8-9, 1929,

at 11:00 p.m. all stations were highly alkaline, and at 1:00 a.m. they were all acid. At 3:00 a.m. they were alkaline again. On August 5, 1930, such a progression occurred at every station save one, but in the opposite direction. The pH was neutral or acid at 6:30 p.m., highly alkaline at 8:30 and acid again by 10:30. Such rapid and wide changes occurring at night and with no regularity cannot be explained with the information at hand.

On August 31, 1928 (Fig. 8) the open water depth series determinations showed the main body of water to be alkaline from surface to bottom. When such conditions occur a lake is commonly termed "alkaline" and from the data of 1929 it would seem reasonable that Ham Lake is of this type, for the twenty-four-hour determinations of that year are also alkaline in sixty-two cases out of a total of seventy-two. However, in 1930, the twenty-four-hour series are somewhat contradictory. On August 5, only twenty-six out of eighty-four determinations were alkaline; August 16 there were seventeen out of ninety-one and September 7 there were twelve out of eighty-four. This makes a total of fifty-five alkaline records for 259 determinations. The open water would be expected to remain most constant, but the fifty-five records include only thirteen from open water, both one and four foot depths. As many determinations were made at these stations as any others. May a lake with such changes be correctly called alkaline? It would appear that whether a shallow glacial lake is alkaline or acid depends upon the season, the weather conditions preceding and at the time of study, and the time of day when determinations are made. The wide horizontal variation at any hour of the day and the striking and inconsistent variation through the day, even from hour to hour, make it unsafe to make generalizations concerning pH or free carbon dioxide without a very large number of determinations made systematically and with a considerable fund of information as to factors involved. This should be a warning against isolated observations which, judging from these data, would be practically worthless.

The data are far from complete. They do, however, show that these variables fluctuate widely and rather inconsistently through the day and night and that the variations have no constant relation to the type of vegetation present or to the stratum in which they occur.

V. VEGETATION AND ENVIRONMENT

The present study, principally descriptive of the environment and vegetation in a lake typical of a large number, was begun as a necessary early step in the cultivation of a field of research as yet almost untouched in Minnesota. Far-reaching conclusions are not to be expected from the study of a single lake. It is possible, however, to point out with considerable certainty, for the locality, the effects of factors, physical and reactional, upon the distribution and development of vegetation.

The original distribution of vegetation in a newly formed lake basin must be due to the physical factors alone, later it is due to the interaction of these and the reactional factors (the effects of the plants themselves upon the environment).

The familiar arrangement of aquatic vegetation in concentric girdles is well shown in Ham Lake, and will be treated in detail in a future paper. For the present purpose the mere fact is sufficient. The dominant factor concerned must be one capable of producing such an arrangement—obviously something related to water depth. Substances in solution, temperature, light, wave action are among the possibilities.

The data presented in this paper show that substances in solution are variable and erratic in relation to both horizontal and vertical distribution. It has been shown that temperature is uniform, both vertically and horizontally, in a relatively shallow body of water like Ham Lake. In a lake deep enough to possess a thermocline there is a difference between top and bottom layers but the thermocline lies at too great a depth to affect the vegetation.

Light, however, shows a definite depth-gradient, with a rapid decrease at first which becomes gradually less rapid downward to a depth of eight feet, where the intensity is approximately one per cent. Since vegetation in Ham Lake ceases uniformly at eight feet it appears that light becomes a limiting factor when reduced to one per cent. This is in agreement with Rickett's observations on Wisconsin lakes but not with the conclusions of Pearsall, who found the plants of certain English lakes limited by an intensity of two per cent. It should be noted that the comparatively slight depth at which the limit is reached is due to organisms and substances in solution in the water, i.e., to a reaction of the vegetation itself. Since light intensity is a limiting factor for plant life and since plants differ in their light requirements, it is reasonable to infer that concentric girdles, directly correlated with depth, are really due to the light gradient. The experimental study of comparative light requirements of aquatic plants, which should furnish corroboration of this inference, is still an open field.

Wave action is effective in the surface stratum only. As a result the shallow portions of the lake are subject to disturbance, but in varying intensity depending on the degree of exposure. Those shores facing the prevalent winds may be swept clean and kept so long after other margins have been built up to late stages in the succession. The floating-leaf plants, especially, are unable to survive in exposed habitats, and the characteristic species of the wave-beaten margins are the more robust of the emergent aquatics. Wave action is thus a disturber of the symmetry of vegetation girdles and a modifying and hindering factor in the progress of succession.

Reactional factors must be considered from the time succession begins following the establishment of the first invaders. The consequent reaction

of vegetation on environment, in turn, affects the further progress of succession. These effects are so important that many, following Clements, consider reactional factors as the only ones concerned in succession. Not all reactional factors are equally important in relation to succession; some perhaps are of no importance at all. The remaining task is to attempt an evaluation.

Light may be reduced in intensity by the plankton, and by substances in solution or suspension, which are almost entirely of organic origin. These must act as retarding factors for the lake as a whole, since by cutting down the light intensity they decrease the depth at which plants can grow. In a given spot, they are equivalent to the effect of deeper water, and thus limit the plant life to earlier successional stages. Flowering plants affect light in a less general way since all grow in comparatively shallow water. The emergent types like *Scirpus* are usually so loosely associated as to permit submerged forms to grow between their stalks. At the other extreme are such plants as *Chara* and *Naias* which grow massed on or near the bottom and cannot affect light conditions. Only those submerged forms which grow profusely and to some size (*Potamogeton compressus* L., *P. amplifolius* Tuckerm., *Elodea*, etc.) are concerned with light as a competition factor. Floating-leaf forms may cover the surface so completely as to shade out bottom species.

Much more important than reaction upon light is the filling-in process due to plants and brought about directly by the accumulation of their remains and indirectly through their effect on the precipitation of carbonates as marl. The analysis of substratum samples gave some unexpected results. Those areas which have been filled and on which the succession has proceeded to the *Zizania* or sedge-mat stage might, with reason, be expected to be composed of almost pure peat. This is in no case true, the highest individual determination being 38.8% organic matter. Surprisingly, this high percentage is found in the deeper water where only *P. compressus* is present. Beneath the *Zizania*, where the bottom has been built up fifteen feet or more, the organic content does not exceed fifteen per cent. All samples with a rather high proportion of organic material have also a high marl content and a small amount of other mineral matter. Those having more than ten per cent organic material almost invariably have at least fifty per cent marl and in most cases considerably more, one *Zizania* soil sample running to 78.8%. All borings in the filled areas showed, at depths of more than a few feet, a mere scattering of plant fragments appearing superficially to be almost pure marl. It would seem, therefore, that decomposition of organic matter goes on rapidly in Ham Lake and that filling is primarily due to the accumulation of marl. The correlation between high organic content and high marl content is noteworthy. The accumulation of so much marl in a lake which lies in a sand plain whose pH ranges from 5.0 to 6.0 seems rather

unusual. There may be some relation to the calcareous drift underlying the sand plain. However, the work of Thiel (1930) shows a greater number of marl deposits in acid than in alkaline drift.

The notable effects of vegetation upon dissolved gases and hydrogen-ion concentration are apparently of little importance in succession on account of thorough diffusion through the water medium. The erratic variation of these factors is such that they cannot be correlated with any part of the lake or any vegetation type. They do, however, have an indirect effect because of their influence upon the organisms of decomposition and upon the precipitation of carbonates. Through the former relation they influence the amount of organic accumulation, and through the latter, the rate of filling by marl.

VI. SUMMARY

1. Ham Lake is typical of a number occurring in pit-depressions of an extensive glacio-fluvial sand plain lying north of Minneapolis, Minnesota. It covers an area of about 160 acres, has a maximum depth of twenty-three and one-half feet and a bottom varying from almost pure sand to marl and highly organic soils.

2. Physical-chemical determinations made in depth series in deep water show that conditions in this regard agree with those of lakes elsewhere of a similar character. Variations throughout the summer in temperature, pH, dissolved oxygen, and carbon dioxide are of a nature to be expected in a shallow lake without a thermocline.

3. The extreme vertical differences of these variables in shallow water is striking at certain stations. For example, the pH at the *Nymphozanthus* station, on July 25, 1929, was 8.9 just beneath the pads, while at the bottom, only two and one-half feet below, it was 6.9. The other variables were in proportion.

4. Studies of horizontal variation in physical-chemical conditions show wide differences among seven stations, representing the several vegetation-types which were studied through the summer of 1929. Practically simultaneous observations show the following ranges: hydrogen-ion concentration, pH 6.75-9.1; dissolved oxygen, (6.3 to 15.3 ppm) 79 to 201% of saturation; free carbon dioxide, 0-2 cc. per liter; total carbon dioxide (free, half-bound and bound), 35 to 62 cc. per liter; temperature 26°-31° C. These variations are not uniform from day to day, since light, temperature, wind and wave action are never the same.

5. Determinations of temperature, pH, oxygen and carbon dioxide were made at seven stations at two-hour intervals through a period of twenty-four hours. One such series was run in 1929 and three in 1930. There were certain obvious correlations among the determinations, and the curves of oxygen concentration and temperature were according to expectation, but for

the most part the variations were so great and so irregular that they are yet unexplainable. On the same day, the variations at the different stations might be uniform or entirely irregular. Again, certain stations might show a parallel variation for a time and then suddenly change apparently out of all proportion to conditions at other stations. The most erratic fluctuations appeared at night and for no apparent reason. For example, the pH might change from highly alkaline to acid in two hours and then back to alkaline again at the next sampling. These series show clearly that isolated observations are practically worthless and that complete information on the character of the habitat, the time of day and weather conditions should accompany all data of this type if a reasonable interpretation is to be made.

6. Because of the great numbers of plankton and because of substances in solution, light penetration is comparatively slight. The average intensity at a depth of two feet is only 15.2% of surface illumination. At four feet the average is 5.2%, at six feet, 1.23% and at eight feet there is no appreciable light. A Secchi disk was visible at depths greater than four feet on but four days in three summers of field work.

7. The characteristic concentric vegetation girdles appearing in lakes must be produced by a factor or factors related to water depth. Since light limits the depth at which plants may grow (in Ham Lake, eight feet; light intensity one per cent) and since individual plants differ in their light requirements it seems reasonable that the vegetation type and therefore the girdles are determined by a light-depth relationship. Wave action is a disturber of symmetry. Temperature and substances in solution are not important because of their uniformity. The reactional factors, dissolved gases and hydrogen-ion concentration, have no direct effect on distribution and succession. They may influence the rate of carbonate precipitation and accumulation and undoubtedly affect the organisms of decomposition, thus controlling the rate of accumulation of marl and organic materials.

8. The effects of the vegetation on the lake itself are most apparent in the accumulation of plant remains and marl. In parts of the lake layers of these materials fifteen to twenty feet in thickness have been built up. Decomposition must be rapid, for soil samples from the filled areas are mostly marl with a low percentage of organic material. Almost invariably, the high organic content of the substratum was accompanied by a still higher marl content.

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THE INFLUENCE OF CLIMATIC AND WEATHER FACTORS UPON THE NUMBERS OF BIRDS ON A DEPOSITING CREEK BANK

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THE INFLUENCE OF CLIMATIC AND WEATHER FACTORS UPON THE NUMBERS OF BIRDS ON A DEPOSITING CREEK BANK

I. INTRODUCTION

The importance of the Class Aves for the investigation of fundamental problems in animal ecology rests upon certain significant facts. First, as a group, birds are very mobile and therefore are freer to react to environmental changes than any other class of vertebrates. Extremes of such reactions are illustrated by the great migrations of birds in the autumn from the north temperate zone southward and by migrations in the opposite direction in the spring. This mobility has increased the difficulties of the study of the ecological relations of birds and has retarded the accumulation of knowledge concerning the organization of bird associations and their environmental relations. Second, birds are relatively large animals which may be identified, even in the field, with relative ease. In comparison with the insects, which also have a high degree of mobility, they are few in species and in individuals, which makes for greater ease in determining ecological relations in the field. Third, there exists a vast amount of detailed information concerning birds which is constantly being added to by enthusiastic observers. The existence of these data is a challenge for the development of methods by which it can be more carefully organized, and particularly methods that will prove valuable in the further study of bird life. Finally, birds are warm-blooded vertebrates the reactions of which may conceivably be of more value in relation to the ecology of the other class of warm-blooded animals (Mammalia) to which man belongs, than would those of cold-blooded animals.

For these reasons, a study of a series of bird habitats at regular intervals through a relatively long period of time was undertaken with the hope that it would give some insight into the problems of animal ecology in general as well as giving new light upon the biocoenoses of which birds are prominent members. It was planned especially to investigate the local motility or change of habitat of birds as the weather changed. For this purpose, a depositing creek bank on the Knapp Farm, five miles from Nashville, Tennessee, on the Elmhill Road, was selected as a specific habitat on which to concentrate, because of its position on the southeast of Mill Creek in a protected spot. On the north and west just across the creek was a high ridge composed of many hills which protected this area from the cold northwest winds of winter. It was warmer both in summer and winter than many neighboring areas. It seemed that such an area would be likely to attract birds when the weather was cold or wet and repel them when the weather was hot or dry.

The method adopted for the study was that of counting the number of

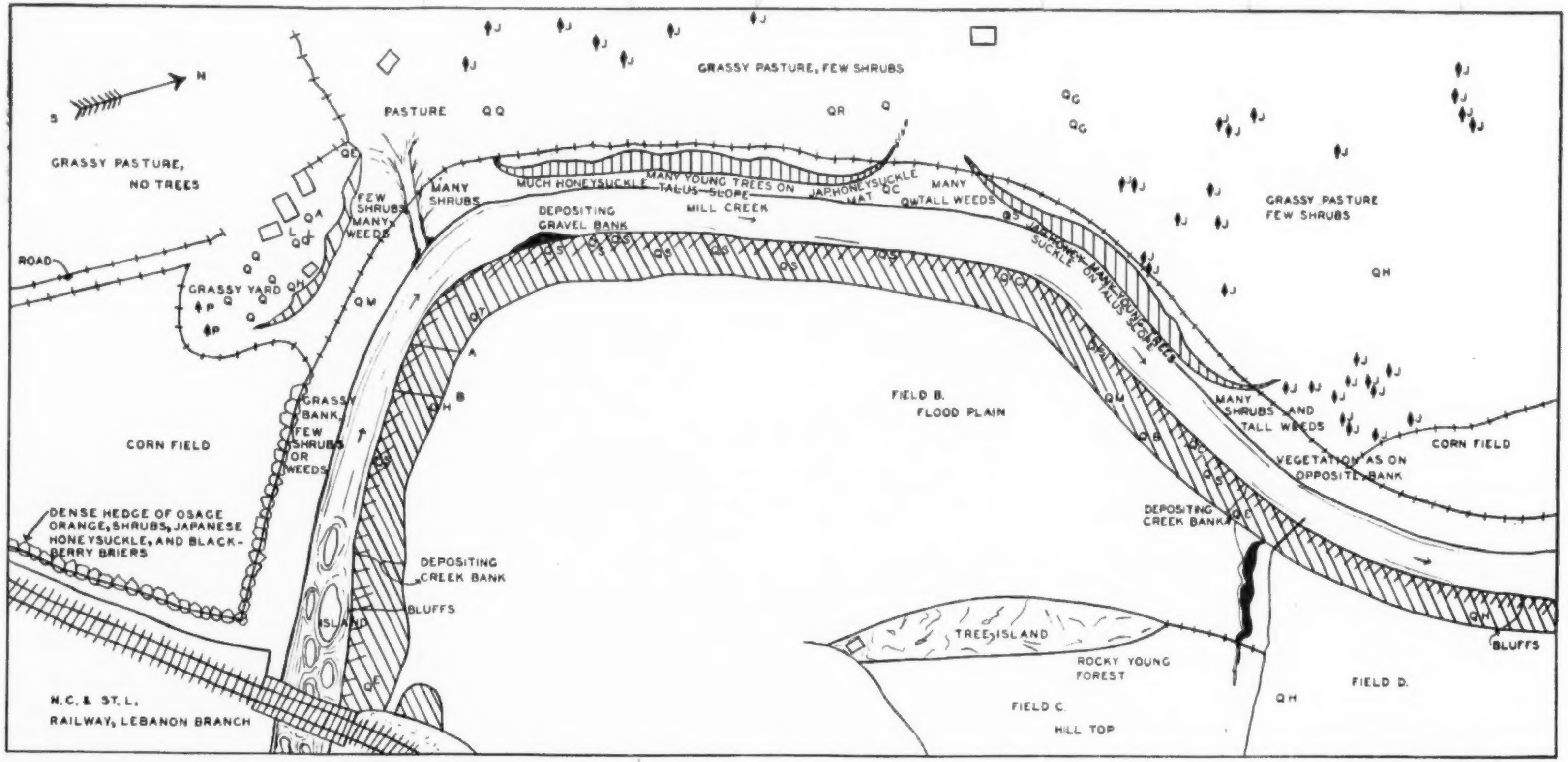

FIG. 1. PLANE TABLE MAP OF THE DEPOSITING CREEK BANK.

DISTANCES DETERMINED BY 40cm LEITZ RANGE FINDER. SCALE, 1 INCH = 50 YARDS. ONLY THE LARGE TREES ARE INDICATED INDIVIDUALLY. SIGNS:
A. WHITE ASH (FRAXINUS AMERICANA L.), B. BOX ELDER (ACER NEGUNDO L.), C. CAROLINA COTTONWOOD (POPULUS DELTOIDES MARSH), E. WHITE ELM (ULMUS AMERICANA L.), G. HONEY LOCUST (GLEDITSIA TRIACANTHOS L.), H. MISSISSIPPI HACKBERRY (CELTIS MISSISSIPPIENSIS BOSC.), J. RED CEDAR (JUNIPERUS VIRGINIANA L.), L. COMMON LOCUST (ROBINIA PSEUDO-ACACIA L.), M. SILVER MAPLE (ACER SACCHARINUM L.), P. SPRUCE (PICEA SP.), Q. YELLOW OAK (QUERCUS MUHLENBERGII ENGELM), R. RED ELM (ULMUS SEROTINA SARGENT), S. SYCAMORE (PLATANUS OCCIDENTALIS L.), T. TEXAS RED OAK (QUERCUS TEXANA BUCKLEY), W. BLACK WILLOW (SALIX NIGRA MARSH.), ▨ - COTTONWOOD, WILLOW, SYCAMORE PLANT ASSOCIATION, +++++ - FENCES, □ - HOUSE, \\\\ - SILVER MAPLE, WHITE ELM ASSOCIATION, |||| - VERTICAL ROCK BLUFFS ACROSS CREEK.

individuals and kinds found in the area on weekly trips made from September 5, 1922 to October 1, 1923. Supplementary monthly field-trips were made from November, 1925 to June 1, 1926. The author wishes to express to Dr. W. C. Allee, under whose direction this study was made, deep appreciation for his kindly interest and stimulating suggestions.

II. CHARACTERISTICS OF THE DEPOSITING CREEK BANK

In view of the problem involved and the nature of the data obtained, the habitat and its environmental complex must be described somewhat in detail.

1. TOPOGRAPHY

The map (Fig. 1) shows the general topographical relations of this area. The depositing creek bank, which was the part of this area studied, averages about thirty-six feet in width with extremes of forty-two and seventy-eight feet. The surface slopes mainly to the northwest. For the most part, it consists of a short, fairly steep, slope next to the creek; and then a longer, more gradual slope which ends finally in a short, steep slope to the nearly level flood plain. However the bank is almost uniformly steep near the railroad, where a small bluff occurs, and almost uniformly of a gradual slope near the middle of the habitat (a synonymous term for the depositing creek bank) where the sharpest bend in the stream occurs. Southeast of the depositing creek bank is a large nearly level flood plain, now in pasture, which is rarely overflowed by the creek. To the southwest, west, and north of the creek is a series of rounded hills which slope gradually to the creek or end abruptly in vertical rock bluffs (indicated on the map by heavy vertical lines).

The creek averages about seventy-eight feet in width at medium high water. In the summer it gets very low. In general, the creek bed is composed of horizontal strata of limestone except in the pools where there is frequently a thin layer of soil on top of the rocks. For this reason, the pools are shallow, none being over thirty inches deep. Between the pools are rapids with gravel, shingle and even larger rocks. When the creek is low, in parts there is much exposed rock. In many places, the water over extensive areas of the rock bottom[1] is not over one or two inches deep. These areas are extensively used by certain birds for bathing and drinking.

2. CLIMATE

A detailed statement of the Nashville climate need not be given here since a summary has been given elsewhere (Shaver, 1928), and its general features are shown in graphs in the body of this paper in connection with the analysis of the influence of climatic factors upon the bird life of this bank. However it seems desirable to point out to what extent the period of

[1] A brief discussion of the geology and soils of this area is given by Shaver (1928, pp. 5-6).

this study (September, 1922, through September, 1923, and November, 1925, through May 5th, 1926) had average weather. This may be conveniently done by bar graphs (Fig. 2).

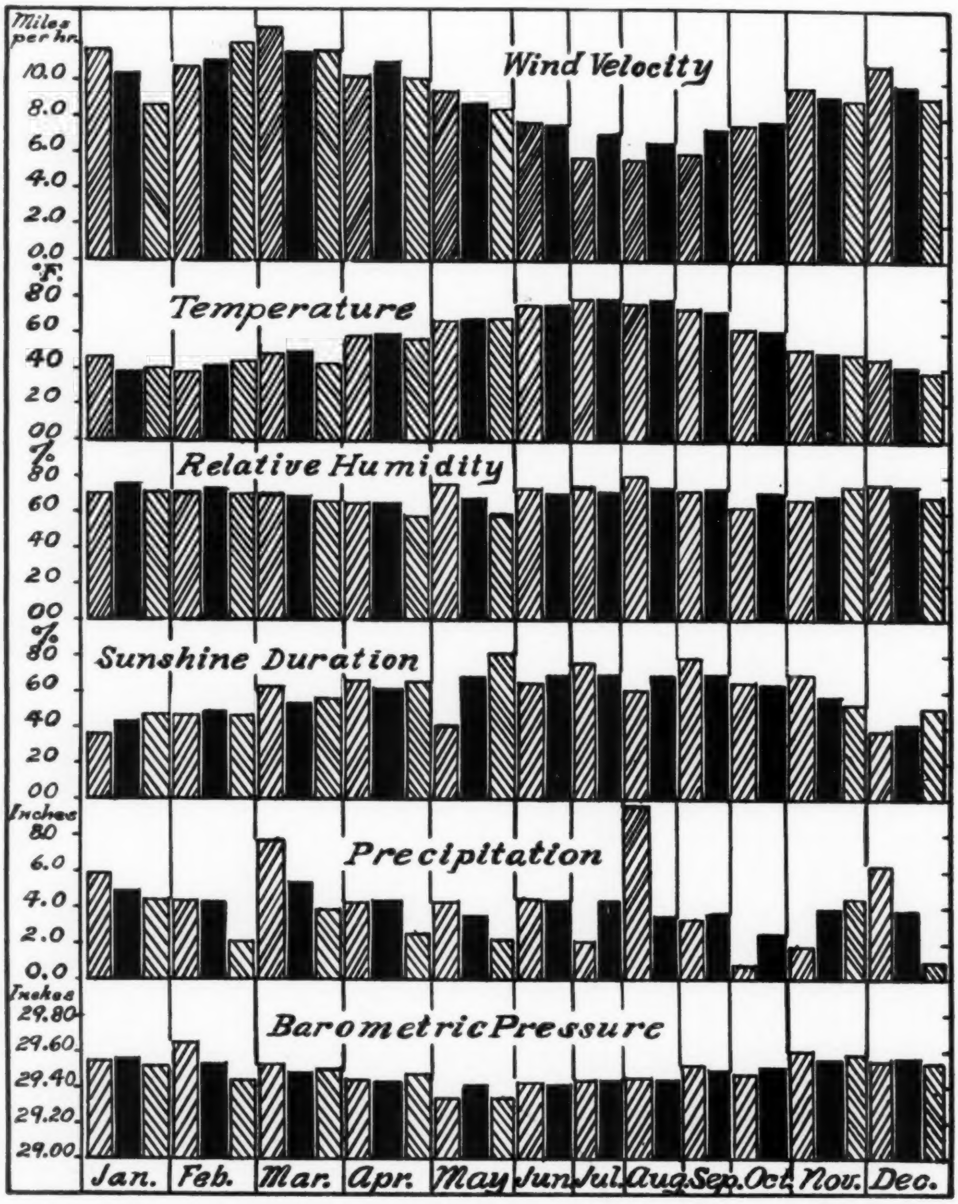

FIG. 2. Climatic Conditions at Nashville, Tennessee (from Nunn, 1923, and from the Nashville Weather Bureau Records). The black bars represent the normal monthly weather or climatic conditions. The bars lined to the left represent mean monthly weather conditions from January 1 through August 31, 1923, and from September 1 through December 31, 1922. The bars lined to the right represent mean monthly weather conditions from January 1 through May 31, 1926, and from November 1 through December 31, 1925.

The information furnished by the graphic comparisons may be summarized briefly as follows: (1) Temperature conditions during the period of the field studies were about average except that December, 1922, and January, 1923, were five degrees or more warmer than usual; (2) relative humidity during August, 1923, and November, 1925, was 5% or more above normal, and in October, 1922; January, 1923; December, 1925; and April, 1926, 5% or more below normal; (3) while precipitation varied a great deal from month to month, there were only three months (December, 1922; March, 1923; August, 1923) with two inches or more rainfall above normal, and four months (November, 1923; December, 1925; February, 1926; and July, 1926) with two inches or more rainfall below normal. August, 1923 had a precipitation of 9.60 inches, the greatest amount recorded for August in fifty-three years (Nunn, 1923); (4) sunshine conditions were nearly normal. There was only one month with 10% or more sunshine below normal and only three months (November, 1922; March, 1923; and May, 1926) with 10% or more sunshine above normal; (5) mean atmospheric pressure was always close to normal. On only one month (February, 1923) was it 0.10 inches or more above normal and on only one month (February, 1926) was the pressure 0.10 inches or more below normal; (6) wind velocity conditions were rather uniform, since no monthly mean was as much as two miles per hour higher or lower than normal.

3. VEGETATION

The vegetation[2] of this habitat (the depositing creek bank) has been worked out by Miss Denison (1925) for the herbaceous plants and by Miss Fitzgibbon (1926) for the woody plants. Fitzgibbon was able to differentiate four main plant associes here. In their order of succession from the creek, they were: (1) the Cottonwood-Black Willow-Sycamore Associes, (2) the Silver Maple-White Elm Associes, (3) the Tension Zone, and (4) the Flood Plain Associes.

The Cottonwood-Black Willow-Sycamore Associes (Fig. 3), next to the creek in position, was made up almost entirely of Carolina cottonwood (*Populus deltoides* Marsh), black willow (*Salix nigra* Marsh) and American sycamore (*Platanus occidentalis* L.) with the black willow the most abundant, the American sycamore the largest, the tallest, and the next most abundant, and the Carolina cottonwood less abundant than the other two. Occasionally box elder (*Acer negundo* L.), green ash (*Fraxinus pennsylvanica lanceolata* (Borkh) Sarg.) and *Sambucus canadensis* L. were found in this first associes. Denison, 1925 (p. 22) lists seven species of herb which she regards as characteristic of this associes, namely:

[2] Plant technical names are based on Asa Gray's New Manual of Botany. 7th edition, New York, 1908.

Marsh Violet (*Viola cucullata* Ait.)

Day Flower (*Commelina communis* L.)

Lady's Sorrel (*Oxalis corniculata* L.)

Nettle (*Urtica chamaedryoides* Pursh.)

Three-seeded Mercury (*Acalypha virginica* L.)

Satin Grass (*Muhlenbergia mexicana* L. Trin.)

Nimble Will (*Muhlenbergia schreberi* J. F. Gmel.)

Besides these seven characteristic herbs, sixteen other species were found to some extent in this associes.

FIG. 3. The Vegetation of the Depositing Creek Bank. To the left is the Cottonwood-Willow-Sycamore Associes. Through the center is a trail on the "bench" made in previous years by grazing animals. To the right are representative trees of the Silver Maple-White Elm Associes. Photograph by Fitzgibbon.

The Silver Maple-White Elm Associes, according to Fitzgibbon (1926), was dominated by the silver maple (*Acer saccharinum* L.) and the white elm (*Ulmus americana* L.) although the box elder (*Acer negundo* L.), the sugar maple (*Acer saccharum* Marsh.) and the ashes (*Fraxinus americana* L. and *Fraxinus pennsylvanica lanceolata* (Berkh.) Sarg.) were common. In all thirty different species of trees and shrubs and eight species of woody vines were found.

The most characteristic herbs of this associes, according to Denison (1925), were:

Spotted Touch-me-not (*Impatiens biflora* Walt.)

Weak Nettle (*Urtica chamaedryoides* Pursh.)

Pale Persicaria (*Polygonum lapathifolium* L.)

Goose Grass (*Galium aparine* L.)

False Nettle (*Boehmeria cylindrica* (L.) SW.)

Indian Pink (*Spigelia marilandica* L.)

Wood-grass (*Muhlenbergia mexicana* (L.)

Altogether Denison (1925) lists eighty-three species of herbs from this associes.

The boundary between the wooded creek bank and the pasture field was called by Fitzgibbon (p. 5) the Tension Zone. The trees there were similar to those just mentioned in the Silver Maple-White Elm Associes with the exception of a great preponderance of hackberries (*Celtia mississippiensis* Bosc.) and an increase in the number of the vines of the Japanese honeysuckle (*Lonicera japonica* Thunb.). Denison (1925) gives a list of twenty-three herbaceous plants found in this zone. Apparently these are the usual types of plants found along field edges, fences and roads.

Besides the plant associes already named, which are characterized mainly by trees, Denison (1925; Shaver and Denison 1928) found two other strictly herbaceous associes: (1) the American Willow-Herb Associes, consisting of an almost pure stand of *Dianthera americana* L., sparsely represented at the water's edge, and (2) a Ruderal Associes which was made up of forty-three different species of stunted, low plants, on gravelly or stony banks.

The extent of some of these five plant associes on the depositing creek bank is indicated on the map (Fig. 1), but their density and height, including growth habits, are not indicated. As creek banks go, this one is rather open in spite of the Japanese honeysuckle vines present. The honeysuckle vines climb the small trees and make a dense mat in their tops but the space on the ground between the trees, because of previous grazing, is not badly matted. Indeed the bank is rather free from very small trees for the same cause. The relatively small size of most of the trees and the relatively open nature of the habitat may be indicated by the graphs given by Fitzgibbon (1926, pp. 50-51). These show for selected quadrats, (1) the number of trees with their heights, (2) the number of trees with their diameters, and (3) the number of trees in relation to their distance from the creek. These data have been condensed for this paper into two figures (Figs. 4 and 5). They indicate clearly the relative openness of the situation and the relatively small size of the trees.

The plane table map of the habitat and its environs (Fig. 1) shows the general nature of the vegetation of the region. The flood plain to the southeast of the depositing creek bank was used for agricultural purposes and so was bare of trees (Fig. 6). During the time of the author's study, it was planted in corn, winter grain, and pasture. The pasture was kept rather closely cropped by cattle, horses, sheep, and hogs. Its vegetation was carefully studied by Ross (1924) by a semi-quantitative method but her lists need not be repeated here. At the eastern end of the flood plain is a small circular wooded area surrounded by fields.

The creek bank on the opposite side from the farm appears to have the same kinds of plants as on the Knapp Farm side but they are much denser except where the horizontal bluffs are exposed. The Japanese honeysuckle

FIG. 4. Plant Succession on the Depositing Creek Bank. The sum total of the trees of Carolina Cottonwood, American Sycamore and Black Willow are indicated by ...... for the normal succession where the creek bank was not wide, and by —.— where the bank was wider. The sum total of the trees of the Silver Maple-White Elm Associes is indicated by ——— for the normal succession and by --- for the succession where the trail occurs on the "bench" (see Fig. 3).

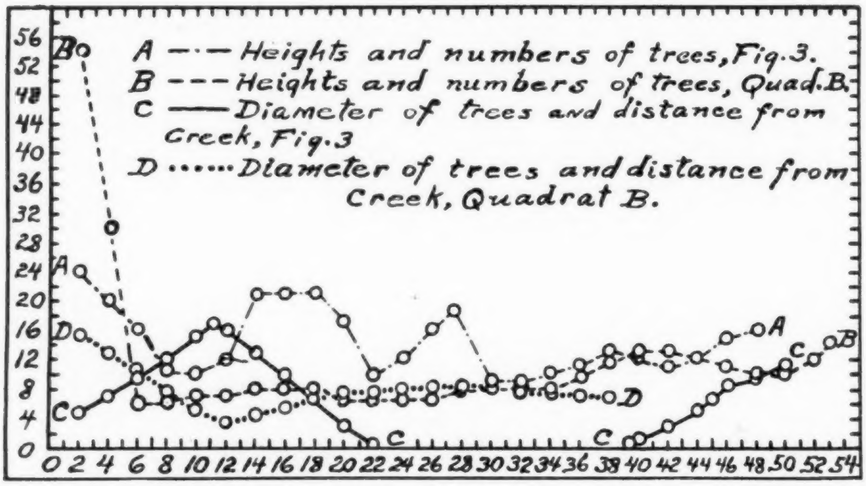

FIG. 5. Plant Succession on the Depositing Creek Bank. The abscissa for graphs A and B represents height in feet of the trees, the ordinate indicates the number of trees. The abscissa for graphs C and D represents distance from the creek in feet while the ordinate represents diameters of trees in inches. The two areas were of the same length (up and down the creek) but of unequal width since each was the width of the creek bank to the cultivated field at two different spots. The first quadrat (curves A and B) was across the area shown in figure 3, while the second quadrat (curves C and D) was in a more normal area.

vines in places there make an almost impenetrable tangle. Back from this tangle the hillside is an open grassy pasture with scattered trees mainly of red cedar (*Juniperus virginiana* L.) and some scattering representatives of other species. All of these trees of any size are indicated on the plane table map (Fig. 1).

At both ends of the area studied, the creek bank on the Knapp Farm side soon becomes an eroding bank with rock bluffs. On the opposite side of the creek at both ends of the habitat, flood plains have been formed and these are now in cultivation. The vegetation other than trees on the hillsides across the creek appears to be similar to that studied by Ross (1924) in the cedar pasture on the Knapp Farm. The detailed list of plants need not be given here. However, it should be noted that the herbs are rather low and

FIG. 6. Cedar Pasture Across from Depositing Creek Bank. On this side is the flood plain. The rounded type of hill ending abruptly in a rock bluff at the creek may be seen.

well grazed except along the ravines (Fig. 1) where they may reach a considerable height and are often exceedingly dense. The general appearance of the cedar field across the creek from the habitat being studied is well indicated by Figure 6.

III. METHODS OF INVESTIGATION

1. BRIEF SUMMARY OF LITERATURE ON METHODS

Census methods have been so widely used in the past that there is a rather extensive literature. For the purposes of this paper it will suffice to review a few typical papers so selected as to show the different methods in use. The species found on a single visit or on repeated visits to an area during the nesting season may be assumed to nest there (Hales, 1880; Wid-

mann, 1909; Hewitt, 1921) and thus a species list may be compiled. Actual nests may be found and counted (Burns, 1901, 1914; Grosvenor, 1916; Whitaker, 1916; Waters, 1916) and a list compiled indicating numbers and relative abundance of nesting species. "The Biological Survey has advocated counting the singing males as the most convenient way of taking a bird census," the count starting at daybreak, in the height of the breeding season—which is regarded as being about June 1 at Washington (Cooke, 1923, 1923a). "Then every male bird can be found in song, and near the nest site . . . it may safely be considered to represent a pair." Cooke recommends that these records should be checked by further observation where possible. While this last method appears to be the very best possible for securing a national census by means of unpaid observers, it should be kept in mind that not all birds have mates during the breeding season, that some birds are polygynous, like the red-winged blackbird, and that the male bird sings most lustily and persistently before nesting.

The works of several authors have a bearing on the value of this method. Allen (1924) found that although a pair of screech owls fed their young seventy-seven individual birds (mainly adults) belonging to eighteen species during the forty-five days of observation, "the number of birds nesting in the sanctuary was but three pairs less than the year before and it was four pairs higher than any other year." Detailed observation on several species indicated that the disappearance of either mate was for a short time only, a new mate appearing sometimes within the same day. The ease with which mates were found suggested the presence of many unmated birds of both sexes. Allen (p. 13) is of the opinion "that nature provides for the catastrophes that may happen to mated birds by causing the immature birds to feel the migrating instinct later, so that they arrive on the nesting grounds after all the adult birds are mated." Burkitt (1924-1925), in his careful ringing (banding) work on robins in Great Britain used combinations of white and black colored metal bands so as to identify individuals. He found each year some mateless males. In 1925, he recorded territory data on fourteen to fifteen pairs and four *unmated* males. Unmated male birds would introduce an error in Cooke's method of arriving at the bird population by multiplying by two the singing males, provided the unmated males sang.

Burkitt (1921) insisted that mating puts a brake or stopper on song, and that there would be little song were it not for unmated males and the recrudescence of song between broods. He also points out that many males find mates slowly and therefore have a prolonged song period. In addition as the season advances there are a number of birds which begin to sing and these singers would be missed in censuses taken in the spring.

Howard (1920, pp. 122-138) associates song with territory and especially with the headquarters tree or bush, with intruding males, and with females,

in the order named. It should be noted that females come last. He also notes (p. 131) the partial or complete suspension of song after pairing has taken place. Saunders (1924) while recording song data on between two hundred and three hundred field sparrows, records, incidentally, suspension of song in one individual, Fl., in 1920, from May 2 to June 14; in 1921, from April 29 to May 24; and in 1922, from May 8 to June 3. "This irregularity in song period is what I have referred to as the individual song period. . . . Every Field Sparrow I have studied individually has exhibited it, though the periods come at different seasons, and last sometimes longer and sometimes shorter times. As previously stated, it is my opinion that these periods of song and silence have a definite relationship to nesting. It is common in many other species as well" (Saunders, 1924, p. 247). Presumably the silent periods were periods of nesting. Thus counts made of singing males of birds like these would not be of any value whatever in indicating the nesting pairs in an area. The Biological Survey method with those birds would be worse than useless. Burkitt (1924-1925) mentions another source of error in these methods. He states "I have had frequent instances in several mating seasons of what appear to be absence of males from their territory of from one to ten days, the shortest periods being the commonest." Absent birds, of course, cannot be counted. Apparently, the evidence indicates the need for caution in the use of the method of estimating nesting pairs of birds by counting the singing males. At best, the method is only applicable to the breeding season, and even then gives no information on feeding ranges, shelter areas, or roosting places.

That the feeding range of some species may be rather extensive is indicated by the work of two observers. Howard (1920) gives two maps showing the territories of six lapwings *(Vanellus vanellus)* but he does not indicate the position of the nest in the territory and therefore it is not possible to determine the extent of the wanderings of the adults from the nest. However, the diagonal of the two longest areas is 513 feet each and that of the next longest one, 464 feet. The largest area apparently includes over 7½ acres although the average of six territories is probably about one-half of this amount. These distances give opportunity for considerable wandering from the nest. Butts (1927) has studied the feeding range of eighty-one individual birds belonging to eight species, using feather dyes and colored leg bands to mark individuals for identification. During the nesting season, red-breasted nuthatches were once found as far as eight hundred feet from the nest and twice, as far as six hundred feet. One pair of song sparrows had a territory of seven thousand square yards around the nest, of which about one acre was available for feeding. In this territory, they could be as far as three hundred feet from the nest. A pair of robins had a territory of two thousand five hundred square yards but sometimes resorted to a common

feeding ground outside of this area. With such large feeding ranges, male birds might not be in the particular area studied at the time of the study. Yet they might nest in the area. This would be another possible source of error in the Biological Survey methods.

At other seasons than the nesting season, the birds of a definite area may wander more. In the autumn there is the host moving southward and in the spring moving northward. Here, a common method for recording migrants (used by Wells W. Cooke in Bird Lore from 1903 to 1916 and continued by Harry C. Oberholser from 1917 to the present) is to record the dates of the first arrival and the date of the last individual seen. Stone (1906) points out some sources of error in recording first arrival dates in migration; two of which touch the method used in this study: (1) The observer may not be in the field every day. The first actual arrivals may be missed and later arrivals recorded as first arrivals. (2) Stragglers may be recorded as first arrivals. Stone's suggestions for combining the data from several stations and for using the time of bulk arrivals are of importance when migration dates are being considered. Chapman (F. M. C. 1914) suggests recording date first seen and number of individuals seen, date next seen and number seen, and date of becoming common in the spring migration. However, in gathering data on the birds present at a definite habitat at a certain time, these suggestions have no value. Similarly, Cooke's view of the value of one observer's data on migration (1907) and his method of rejecting early and late dates (1908) may be dismissed as not pertinent to the problem under discussion.

Apparently the wanderings of birds are quite variable. Some have a very restricted range (Musselman 1923; May 1924) while others may wander widely (Thomson 1926; Wetmore 1926; Butts 1927).

Evidently counts of individuals by species must be made on each field trip to find out the bird population of a particular habitat. Grinnell (1914) used this method of counts on daily trips over the Berkeley campus, but Forbes and his associates (Forbes 1907, 1908; Forbes and Gross 1921, 1922, 1923) have made some of the best statistical studies on the local distribution of birds. The earlier method used by Forbes and his associates (1907) was that of direct counts of individuals by one observer while an accompanying observer counted paces. The two observers were about thirty yards apart and walked parallel to each other across the country. Later, distance traveled was recorded by a mechanical counter. All of the birds seen either on the wing over the habitat or perched in the habitat were recorded on a strip 150 feet wide. Detailed data on temperature, wind and other weather phenomena were recorded, but not published. Presumably, detailed data on each habitat were noted but in the published articles this was all grouped under the crop concerned. For example, under the heading of orchards (1921) were

listed all birds found in orchards irrespective of whether these were carefully cultivated, in sod, in weeds, or badly grown up in shrubs and young trees. Furthermore, the orchards may be newly planted or long-standing and may therefore be of very small trees or of tall and partially decayed trees. However, Forbes recognized that the detailed nature of the habitat was significant for he specifically states (1908, p. 8): "It was, in fact, very obvious that a well-kept orchard, in which the ground was free from tall grass or bushes, was a rather poor place for birds (see Plates 1 and 2) but that one in which grass and herbs grow freely, and especially one in which dew-berries and other shrubs were abundant, was a situation preferred above all others. It is this kind of ground-cover and the trees taken together—the latter useful to some for nesting and to nearly all for shelter against storms and for refuge from their enemies—which make up a complete bird orchard, answering to the essential needs of the orchard birds of this discussion." The birds found in wheat fields were also grouped together in spite of the fact that some were recorded when the wheat was young and some when it was mature. The observation trip was continuous across the country; no return trip over the exact route of a previous trip being made. Thus exact seasonal effects could not be noted.

Allen (J. A. A. 1908) has criticized Forbes' (1908) paper on the ground that comparisons between studies made in southern Illinois in June and northern Illinois in August cannot be satisfactory. So Forbes and Gross in their later studies (1922, 1923) used the method of two week's study in southern Illinois, then two weeks in central Illinois, and then two weeks in northern Illinois; this sequence being repeated throughout the period of the study.

From this brief literature review, it is apparent that the method of securing data of most significance for the purposes of this study is that of making field trips to the area under consideration at as nearly equal time intervals as possible and recording the species and number of individuals present on each trip.

2. THE FIELD TRIP

The data were collected on weekly field trips during thirteen months (September, 1922, through September, 1923) and on monthly trips for six months (November, 1925, through May, 1926). Usually the weekly trips came exactly a week apart; on Saturdays, except one on Friday, seven on Sunday, two on Monday, and two on Tuesday. The first three of the monthly trips were five weeks apart and the next three, four weeks. On the monthly trips, data were collected at three different times of the day: (1) in early morning; (2) near noon; and (3) in the afternoon. Thus the data were reasonably evenly spaced throughout the period of study and might be expected to show seasonal and weather effects. A standard route was followed

through the area studied so as to make the data comparable. For the same reason, an attempt was made to study the area about the same time of day each week of the weekly field trips, but this was not always possible on account of the varying time demands of other situations.

Each week (just preceding the field trip) rough estimates were made of the weather under the following heads: wind strength and direction, cloudy or clear, raining or snowing, temperature in degrees Fahrenheit. Instruments for getting quantitative data on these factors were not available but the United States Weather Bureau at Nashville kindly furnished data for Nashville (five miles from the area studied).

On each trip, every bird seen on the depositing creek-bank was listed under the proper species at the time seen, in a field notebook. Birds noted flying over this habitat were listed separately in the notes, but, with the exception of a few soaring birds—mainly vultures and hawks—have not been considered in this report. The birds seen on the creek adjoining the area studied, those on the opposite bank of the creek and those on the flood plain to the southeast of the habitat have been separately recorded in the field notebook, but have not been considered in the part of the study here presented. Song, nesting activity and feeding activity were recorded when it was possible to obtain accurate data on these. However, it should be pointed out that there was little nesting in this habitat. It was used apparently by birds primarily for other purposes. In the field, a field glass was carried for use in identifying specimens and a small bore shotgun for collecting specimens difficult to identify in the field.

Thus data were collected on: (1) the kinds and numbers of species present in the habitat, (2) the number of individuals of each species present, (3) the kinds and number of individuals in flight over the area, (4) the kinds and numbers of birds in each of the main areas adjoining the one studied, (5) the number of individuals of each species in song in the area studied and in adjoining habitats, (6) the number and kind of birds nesting in the area, and (7) observed feeding habits.

IV. RESULTS OF THE FIELD STUDIES

The notebook data on the number of individuals of each species present in the habitat were tabulated by seasons. As an example of this primary tabulation, Table I is presented in detail.[3]

The mean number of individual birds present for the entire autumn quarter was 32.85 ± 2.47 and the mean number of species was 11.62 ± 0.91. This is an average of 2.83 individual birds for each species. Since all of the rest of the primary tabulations were made in a similar way to the one for

[3] Bound copies of the primary tabulation of all birds and environmental factors, as well as the calculations involved in this study, have been deposited in the libraries of the University of Chicago, Duke University, and George Peabody College for Teachers.

autumn birds, it does not seem necessary to present them in detail. Instead brief summaries may be given (Tables II-VII).

TABLE I. *Autumn birds of the depositing creek bank, 1922.*

NAME OF BIRD	NUMBER OF BIRDS PRESENT												
	September					October				November			
	5	12	18	23	29	7	15	21	28	5	12	19	25
Cooper's Hawk*										1			
Eastern Red-tailed Hawk				1									
Eastern Sparrow Hawk												1	
Eastern Mourning Dove					1								
Yellow-billed Cuckoo	1	1											
Eastern Screech Owl			1										
Eastern Whip-poor-will					1								
Northern Flicker		1		4	2		1		3	4		1	2
Red-bellied Woodpecker							1						
Red-headed Woodpecker	1												
Eastern Hairy Woodpecker		1		1	1				1				
Northern Downy Woodpecker			1				2						1
Eastern Phoebe						1	1						
Eastern Wood Pewee		1		1									
Blue Jay	1	1	1	2	1	1	1	1					
Carolina Chickadee	2		2	3	3			2	2	3		1	
Tufted Titmouse		1		3	3				2	2		1	
Brown Creeper													1
Eastern Winter Wren						1	1						
Carolina Wren	7	2	2	4	1	1	3		3				4
Eastern Mockingbird				1			1		1				1
Catbird	2	3	3	1	1								
Brown Thrasher	4	2	1	1									
Wood Thrush	1		1	1									
Eastern Bluebird										2			
Golden-crowned Kinglet							5		2	15		1	1
Eastern Ruby-crowned Kinglet				1									
White-eyed Vireo	5		2										
Black and White Warbler	1		2	1	1								
Magnolia Warbler			5	4	3	1							
Myrtle Warbler											4		
Black-throated Green Warbler					1								
Chestnut-sided Warbler	1			4	2								
Louisiana Water-thrush	2		2	1									
Maryland Yellow-throat		2			4	1							
American Redstart	3	3											
Ovenbird				3	1			1					
Eastern Red-winged Blackbird							12						
Bronzed Grackle	1			1	1								
Indigo Bunting		1	2	4	6		1						
Eastern Cardinal	8	2	5	1	1	2	2			3	2		3
Eastern Goldfinch										3			
Red-eyed Towhee			2		4	1				2			
Eastern Vesper Sparrow									1				
Carolina Junco										1			4
Field Sparrow								1					
White-throated Sparrow								5	21	27	14	11	38
Eastern Song Sparrow									2	1	3	5	2
Total Individuals	40	21	32	43	38	9	31	10	38	64	23	21	57
Total Species	15	13	15	21	19	8	12	5	10	12	4	7	10

*Common names are those given in the A. O. U. checklist, 1931 Edition, where the corresponding technical name will be found.

TABLE II. *Summary of the winter birds of the depositing creek bank, 1922-1923.*

NAME OF BIRD GROUP	NUMBER OF BIRDS PRESENT												
	December					January				February			
	2	9	16	23	30	6	13	20	27	3	10	17	25
Total Individuals	38	11	12	16	21	34	19	6	24	9	7	38	19
Total Species	7	5	7	9	8	9	7	3	8	5	4	16	6

The mean number of individual birds present for the entire winter quarter (Table II) was 19.54 ± 2.00 and the mean number of species was 7.23 ± 0.59. This is an average of 2.71 individual birds for each species.

TABLE III. *Summary of the spring birds of the depositing creek bank, 1923.*

NAME OF BIRD GROUP	NUMBER OF BIRDS PRESENT												
	March					April				May			
	3	10	17	25	31	7	14	21	29	5	13	19	26
Total Individuals	31	10	18	21	29	26	15	13	23	42	56	10	19
Total Species	5	4	11	10	8	9	8	9	13	25	22	7	9

The mean number of individual birds present for the entire spring quarter (Table III) was 24.08 ± 1.41 and the mean number of species was 10.77 ± 1.10. This is an average of 2.24 individual birds for each species.

TABLE IV. *Summary of the summer birds of the depositing creek bank, 1923.*

NAME OF BIRD GROUP	NUMBER OF BIRDS PRESENT												
	June					July				August			
	2	9	16	23	30	7	14	21	28	4	11	18	25
Total Individuals	31	25	33	22	17	34	13	32	28	28	23	13	14
Total Species	9	11	16	8	10	13	8	11	11	13	11	7	9

The mean number of individual birds present for the entire summer quarter (Table IV) was 24.08 ± 1.41 and the mean number of species was 10.50 ± 0.48. This is an average of 2.28 birds for each species.

TABLE V. *Summary of September birds of the depositing creek bank, 1923.*

TOTAL SPECIES PRESENT				TOTAL INDIVIDUALS PRESENT			
Sept. 1	Sept. 8	Sept. 15	Sept. 22	Sept. 1	Sept. 8	Sept. 15	Sept. 22
13	15	7	17	21	26	10	51

The mean number of individual birds present in September, 1923, was 27.5 ± 5.06 and the mean number of species was 13.0 ± 0.59. This is an average of 2.12 birds for each species.

TABLE VI. *Summary of the winter birds of the depositing creek bank, 1925-1926.*

Name of Bird Group	Number of Birds Present								
	November 28			January 3			February 6		
	Trip 1	Trip 2	Trip 3	Trip 1	Trip 2	Trip 3	Trip 1	Trip 2	Trip 3
Total Species	6	11	9	10	8	9	6	7	5
Total Individuals	11	21	17	22	30	35	11	8	7

The mean number of species of birds per trip during the winter (Table VI) was 7.89 ± 0.43 and the mean number of individuals was 18.00 ± 2.09. This is an average of 2.28 individuals for each species.

TABLE VII. *Summary of the spring birds of the depositing creek bank, 1926.*

Name of Bird Group	Number of Birds Present								
	March 6			April 7			May 5		
	Trip 1	Trip 2	Trip 3	Trip 1	Trip 2	Trip 3	Trip 1	Trip 2	Trip 3
Total Species	6	4	4	12	14	11	32	28	22
Total Individuals	12	8	8	24	30	18	97	77	63

The mean number of species of birds per trip during the spring of 1926 (Table VII) was 14.76 ± 2.19 and the mean number of individuals 34.44 ± 7.01. This was an average of 2.54 individuals for each species.

Considering together all the birds found during the entire study, it is found that eighty-eight species were present at some time on the depositing creek bank. However, the mean for each field trip was only 10.51 and the mean number of individuals 25.87. This gives an average of 2.46 individuals per trip for each species. This last fact indicates the relatively non-gregarious relations of the birds present. With the exception of the gregarious white-throated sparrows, which were common from October 15 to April 15, there were present only seven times during the study, as many as five individuals of the gregarious species in the entire habitat.

V. ANALYSIS OF THE FIELD RESULTS

The preceding primary tabulation was examined to see what groupings of birds could be made that might be related to climatic factors. Ordinarily, birds are regarded as permanent residents (P. R.) when they occur in the region throughout the year, summer residents (S. R.) when they are present only during the summer, winter visitants (W. V.) when they are found only during the winter, and migrants (M.) when they pass through in the spring,

fall, or in both the spring and fall (Chapman, 1912). Since these groups are generally considered as being related to climate, and in quite different ways, it was decided to try this classification of the data.

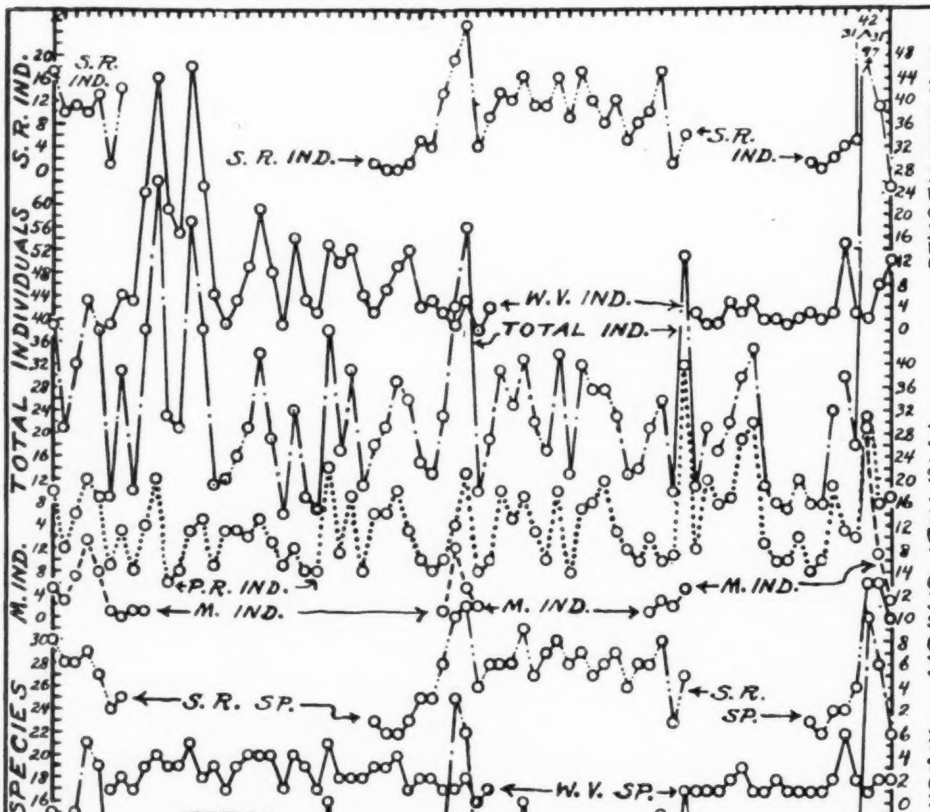

FIG. 7. Groups of Birds of the Depositing Creek Bank. M. IND., migrant individuals; M. SP., migrant species; P. R. IND., permanent individuals; P. R. SP., permanent resident species; S. R. IND., summer resident individuals; S. R. SP., summer resident species; TOTAL IND., total individuals; TOTAL SP., total species; W. V. IND., winter visitant individuals; W. V. SP., winter visitant species. The figures on the y-axis refer either to the number of species or the number of individuals as indicated. At the lower right of the abscissa is indicated the days on which three trips per day were made. Here N. is for November, J. for January, F. for February, M. for March and A. for April.

The results are expressed in a graph (Fig. 7) together with the curves of total species and total individuals. On examining these curves, one is struck by their saw-toothed fluctuations. These may be due to weather or other fluctuating conditions but manifestly they cannot be due to climate. The slower, more gradual changes—if they are present—may be due to climate or to other causes. What is needed is a method of separating the slow and gradual changes from the more rapid, fluctuating ones. Yule (1924, page 200) has suggested a method for separating the slow, gradual trend of a curve from the saw-toothed fluctuations. It is by so smoothing each curve that it is practically free from small fluctuations.

So the different curves were smoothed by formulae determined by trial and error. The details of constructing and using these formulae have been given elsewhere (Shaver and Walker, 1931) and need not be repeated here. It will be sufficient to state that the following formulae were found to be satisfactory: $\frac{a + 2b + 3c + 4d + 5e + 4f + 3g + 2h + i}{25}$ for species and

$$\frac{a + 2b + 3c + 4d + 5e + 6f + 7g + 6h + 5i + 4j + 3k + 2l + m}{49}$$

for individuals. However, it should be mentioned that the data collected on the three-trips-per-day excursions (Nov. 28, 1925, through May 5, 1926), although smoothed by the formulae given above, differed from the methods given above in that the data for corresponding parts of days were smoothed together. For instance, the data for P. R. Sp. for the first morning trip on November 28 (at 7:30 a.m.) were smoothed with that from the first morning trip on January 3 and with that from the first morning trip on March 6, *et cetera*, rather than with the second morning trip on November 28, the third morning trip on November 28, and the first morning trip on January 3. It appeared that this method of smoothing would be comparable to that used with the other data as given above.

A comparison of these smoothed curves (Fig. 8) in detail does not seem worth making since they are obviously quite unlike. Winter visitants are only present during the winter when the only other birds present are permanent residents. In the autumn, winter visitants arrive before the departure of all the summer residents and migrants, and, in the spring, they linger on until after the arrival of these groups. In the summer, only summer residents and permanent residents are present, and in the spring and autumn, migrants are added. Thus, the group of total birds is controlled at one season by one group and at other seasons by others.

The deviations of the unsmoothed curves from the smoothed ones may be assumed to be due to fluctuating causes (Yule, 1924, pp. 200-201). They may be graphed for comparison with each other and with weather phenomena (Fig. 9).

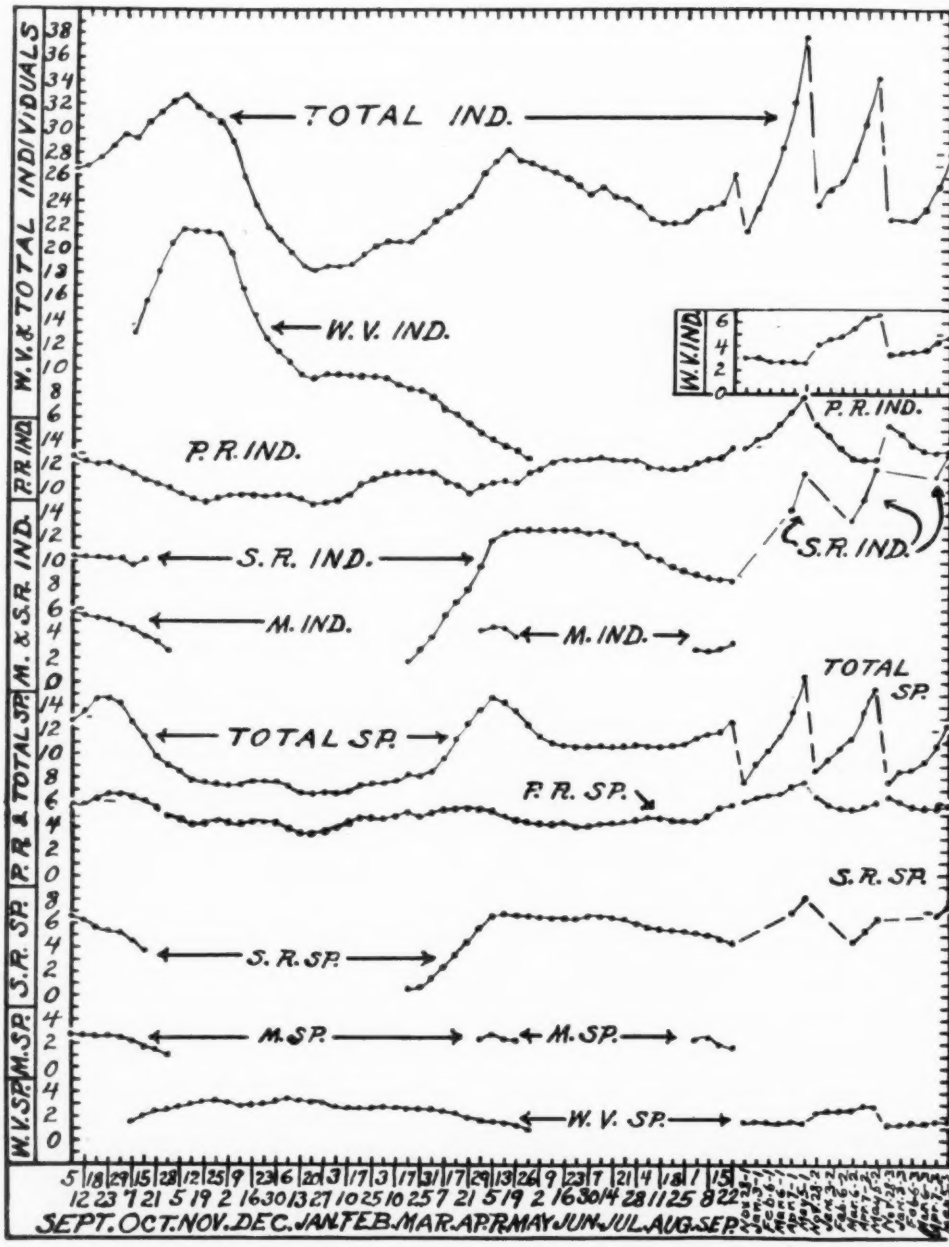

FIG. 8. Smoothed Curves of Bird Groups, Depositing Creek Bank. The legend is the same as in Figure 7 with minor exceptions. At the lower right-hand corner of the abscissa, the different trips taken on the same day are indicated by 1 after the date for the first trip, 2 for the second trip and 3 for the third trip.

While it is not necessary to compare these different curves of deviations (Fig. 9) in detail with one another for the purposes of this study, yet a brief comparison may facilitate the later work. When any one of the curves is compared with the other curves, certain things appear that are quite aston-

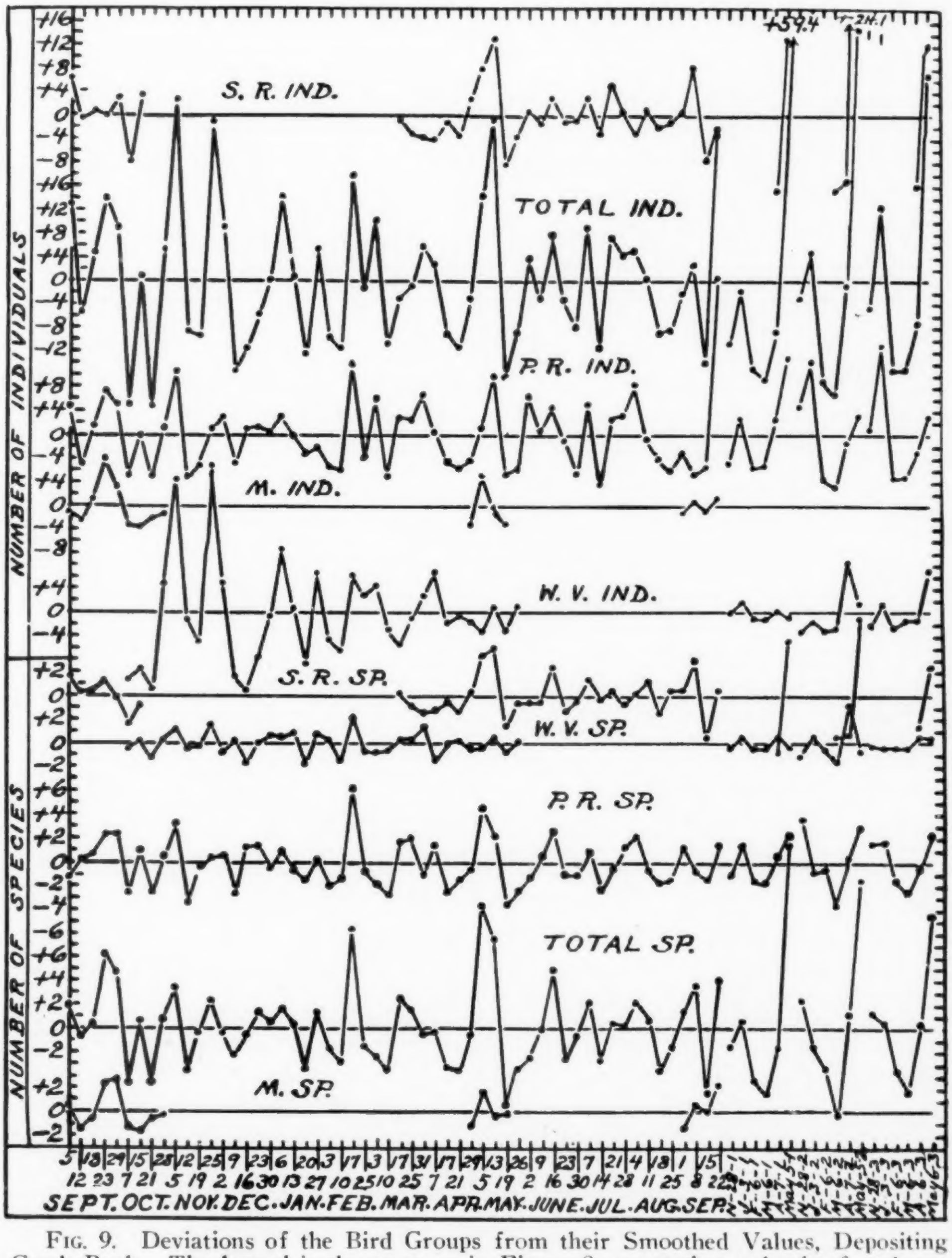

FIG. 9. Deviations of the Bird Groups from their Smoothed Values, Depositing Creek Bank. The legend is the same as in Figure 8 except that only the first letter is used for the months in the right-hand corner of the abscissa; thus agreeing in this last respect with Figure 7.

ishing. (1) When any single curve ascends, any other curve that may be considered ascends and when any single curve falls any other curve also falls (but not necessarily in proportion) about ninety-five per cent of the time. (2) Most of the weeks that do not agree with the above statement fail by two or less birds. (3) If it is assumed that errors as great as two birds

(two species or two individuals) may be inherent in the census method employed, this result appears: of the 457 chances (number of trips, times number of categories minus one), only nineteen or less than five per cent differ by more than two. The fewness of these exceptions is quite surprising and indicates so clearly the very great tendency of all of the curves (Fig. 9) to rise and fall together that a statistical comparison is not needed.

The entire preceding analysis suggests that permanent residents, summer residents, winter visitants, and migrants are quite differently related to climate or some slow-acting phenomena, but that they are similarly related (but not to the same degree) to weather or other fluctuating conditions. Therefore in studying climate, every single group must be compared with every single climatic factor but in studying weather only one group of birds need be used until some definite relationship is discovered. This will greatly facilitate the work.

VI. THE EFFECT OF CLIMATIC INFLUENCES UPON THE BIRD POPULATION OF THE DEPOSITING CREEK BANK

The interesting field data presented in the preceding section is now to be analysed in relation to climatic influences. Climate is used in the sense given by Hann (1908, p. 1) of *average* or *mean* weather.

The commonly observed seasonal rhythms of bird activities appear to be associated with climatic factors. Of these activities, migration has apparently been most studied from this standpoint. Cooke (1910) pointed out the very great importance of *average weather* in bird migration and the relative unimportance of fluctuating weather phenomena. One year it may seem that storms hold back the migrants while another year they may continue in spite of weather conditions. Similarly, the great mass of the early work dealing with weather effects on migration presents conflicting data. In 1916, Bretscher, as the result of a careful statistical inquiry based on 10,000 single observations of migration, came to the conclusion that mean daily temperature was the most significant factor.

Cooke (1913a) later changed his views concerning the unimportance of weather conditions in migration, probably due to Eagle Clarke's thorough analysis of the situation in England (1912), and Bretscher's statistical methods have not been considered any too kindly (Thomson, 1926, pp. 111-112). The papers of these investigators are important in that they call attention to the significance of climate in contrast to the fluctuating conditions of ordinary weather.

Of the activities of birds other than migration, those associated with the nesting season appear to be most closely related to climate. This association is so close that many of the popular bird books give nesting dates under each species along with identification characters and range.

Many of the activities of birds seem to be rhythmical in that they occur each year at about the same time. With regard to migration, Bretscher (1916, p. 317) says, "dass die Vögel nicht der Wärme wegen, sondern deswegen siehen, weil die Zeit hierfür gekommen ist, hier eine willkommene Bestätigung." Wachs (1926, p. 604) develops with much skill the view that migration is due to an inner physiological rhythm specific for the species. The relation of this rhythm to present climate is imperfectly known both in the case of migration and nesting activity.

In the case of the movements of bird species and individuals within a restricted area, the author has been unable to find any published analyses based on climatic factors, and yet this seems to be a significant field for investigation. The very great difficulty of an investigation of this type is indicated by the apparent lack of objective data on man (Hann, 1908), although subjective data are common, and the varying views as to the influence of climatic factors on bird migration (Thomson, 1926, pp. 101-114). Even with cold-blooded animals the difficulties are very great. For instance, Shelford (1926) indicated that a set of sixty combinations of temperature and humidity must be used, with each generation, in experimentation with insects to secure worth while results. He says that this must also be supplemented by a corps of observers working in the field.

In spite of these difficulties, the author has attempted to analyze his data in relation to the various climatic factors of temperature, relative humidity, precipitation, light, wind and atmospheric pressure.

1. TEMPERATURE EFFECTS

In view of the importance ascribed to climatic temperature in migration by Cooke (1913) and Bretscher (1916) in their earlier papers, and in distribution by Allen (1871) and Merriam (1894), it was thought that some significant data might be discovered on the relation of temperature to the local movements of birds. Normal temperatures are considered since the normal is a mean of data that has extended over a relatively long period of time (Milham, 1923) and thus closely approaches the temperature factor of climate. The curve of any normal temperature whatever, is approximately parallel to the curve of daily normal temperature as is well shown in Figure 10. In this study, these temperature factors were used: (1) Monthly normals, (2) monthly normal maxima, (3) normal maxima for the days of the study, (4) monthly normal minima, (5) normal minima for the days of the study, and (6) daily normals for the days of the study. The data for these curves were taken from Nunn (1923) and from the Nashville Weather Bureau records. In addition, the mean monthly temperatures for the months of this study were graphed in order to see to what extent the year studied was a representative one. Also, a nine-point-weighted (formula:

$$\frac{a + 2b + 3c + 4d + 5e + 4f + 3g + 2h + i)}{25}$$

curve was constructed from the median weather data for the actual hours of field study. This last curve is approximately parallel to the curve of mean monthly temperature for the months of this study (Fig. 10). Both of these last curves indicate that this period of time varied only slightly from the normal or climatic temperature and therefore may be taken as representing this phase of climate.

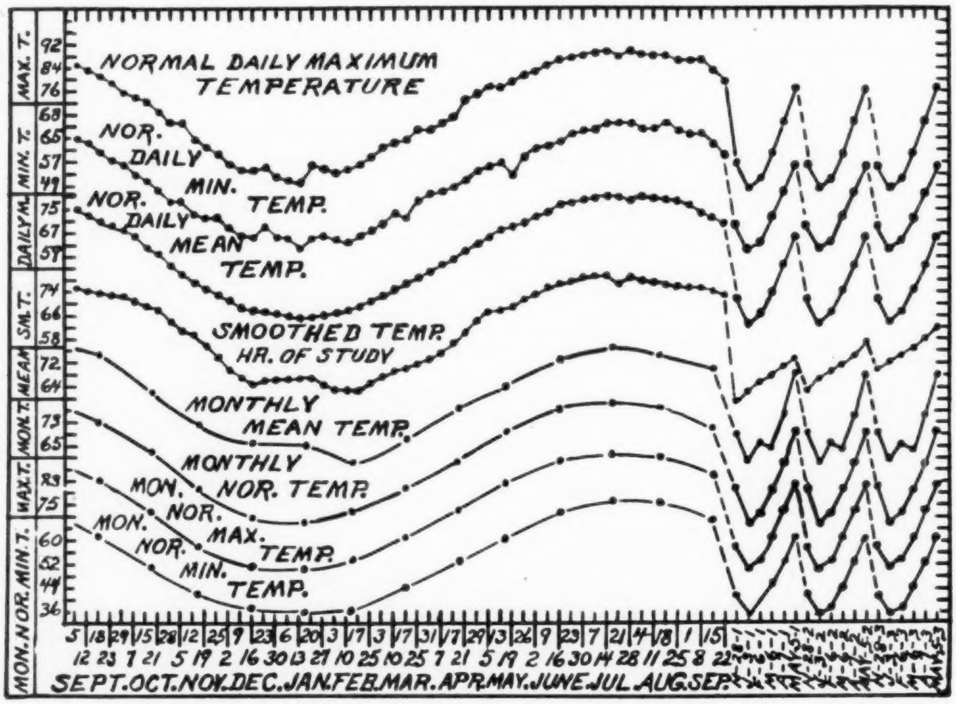

FIG. 10. A comparison of Smoothed Temperature for the Hours of the Field Study and other Temperature Relations for the Nashville Section. The abscissa has the same legend as in Figure 9.

Since every one of these temperature curves is approximately parallel to every other one, it is necessary in this study to compare the curves of bird abundance with only one temperature curve. The choice of curves is immaterial. For this study, the nine-point-weighted-smoothed curve of temperature of the hours of the field study was selected for comparison. It will be recalled that the smoothing process actually produced a curve from fluctuating weather conditions (Fig. 10) closely approximating that of climate. In this comparison, the smoothed curves of numbers of individual birds will be used in preference to the smoothed curves of numbers of species because the curves of number of individuals really represent species curves weighted according to the number of individuals of each species present during the period of study, and secondly—with the exception of winter visitants—the

species curves are approximately parallel to the corresponding curves of individuals.

At first there appeared no basis for seasonal treatment of the data. However, many trial divisions were made and the data examined—not only in relation to temperature but also with reference to the other climatic and weather factors. On the basis of these preliminary studies, the equinoxes were selected as the best division points. Considering the period from March

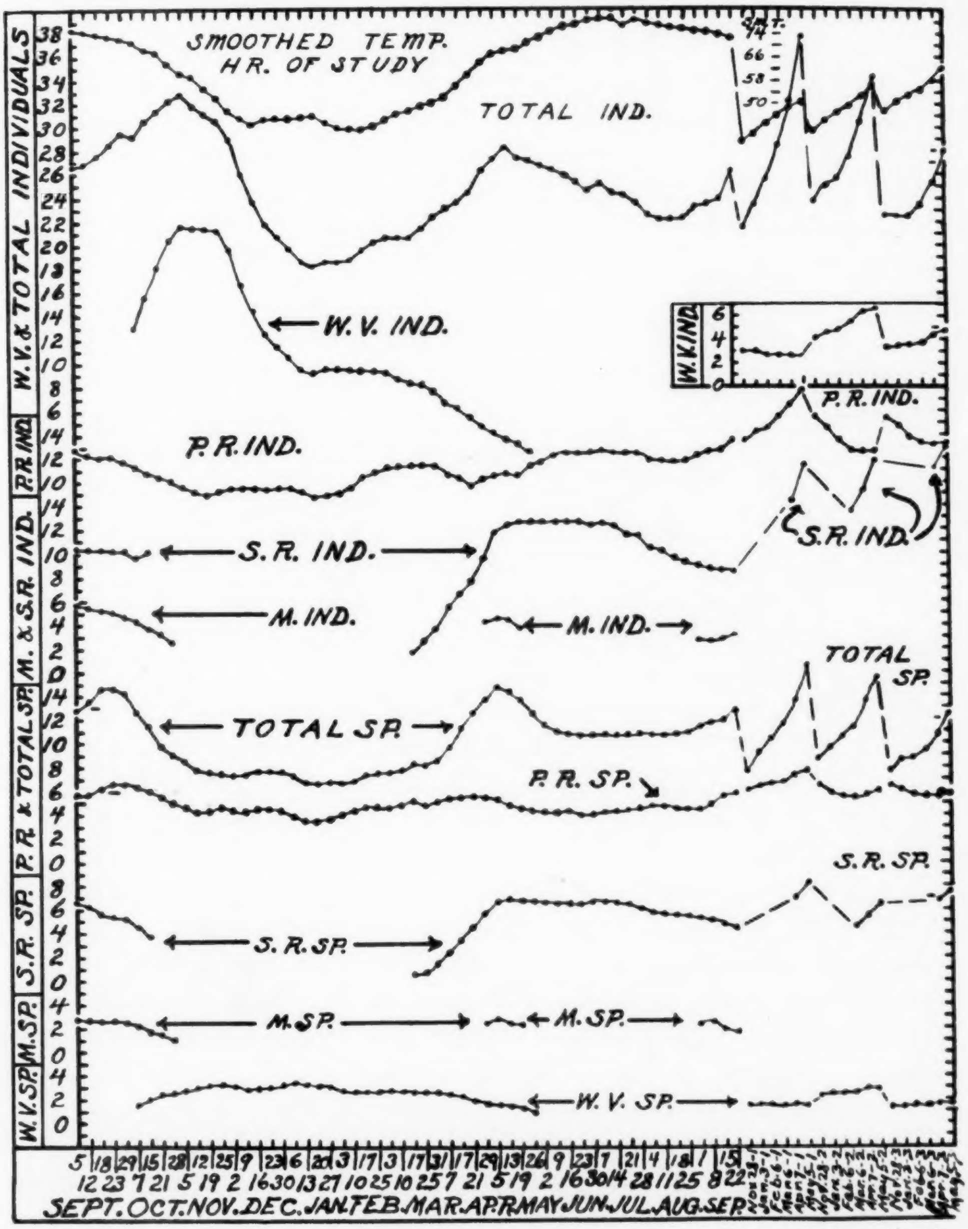

FIG. 11. Comparison of All Bird Groups with Temperature. Legend as in Figures 8-9.

21 to September 21, it is readily apparent that all of the birds together (total birds, Fig. 11) show a very similar curve to that of temperature with a minimum in mid-winter and high points in the autumn and spring. Summer residents and migrants are absent, winter visitants (individuals) have a similar curve to that of temperature in the autumn and early winter, but in late winter the relation is a negative one. Permanent residents show little relation. During the spring, this same relation is maintained with total birds but in the summer period the relation is reversed, the minimum numbers of birds occurring near the time of maximum temperature. Summer residents show little relation to temperature since their maximum occurs in May and June while that of temperature is in July. Permanent residents are little affected.

Another, and in some respects a more satisfactory method for comparing variations of bird numbers with variations in temperature or other climatic factors, is by means of Pearson's coefficient of correlation. This and other statistical methods appear worthy of more general use in ecology than have been the case in the past. The results of the application of this method in comparing bird numbers and temperature, are shown in Table VIII. Mi-

TABLE VIII. *The relation between smoothed temperature and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind.	Temperature at hr. of study	0.674 ± 0.059	-0.409 ± 0.095
P. R. Ind.	Temperature at hr. of study	-0.247 ± 0.107	-0.247 ± 0.107
W. V. Ind.	Temperature at hr. of study	0.554 ± 0.078	....
S. R. Ind.	Temperature at hr. of study	....	0.008 ± 0.114

grants are not given as a group because there is not enough material for statistical treatment. However, they have been included under total birds. While some of the coefficients of correlation are low as compared with their probable errors, they are all consistent with general observations in the Nashville area. For example, there are more individual birds but less kinds of the group, winter visitants, when the average temperature is highest, *i.e.*, in the early fall and late spring. At these times, there are many individuals, especially of sparrows, migrating. Most of these individuals winter south of Nashville but some few remain all winter. Also many winter visitants, represented by few individuals, arrive late in the autumn and depart early in the spring. Permanent residents have a negative relation to temperature at all times, but it is very slight. In both the early and late summer, migrant individuals of permanent resident species, which occur on the depositing creek bank throughout the year, pass through or take the place of individuals of the same species which pass northward. The net result is to make permanent

residents appear more numerous at these times than in midsummer when the temperature is highest. This is probably the reason for the negative correlation for permanent residents in the summer half of the year.

The fairly high coefficient of correlation for total individuals for the winter half of the year is due to the influence of winter visitant individuals and especially the newly arriving summer residents in late spring. In the fall it is due to fall migrants, late departing summer residents and especially to the great influx of winter visitants at this time. The negative correlation for total individuals with temperature for the summer half of the year is largely influenced by the presence of migrants and winter visitants in late spring and early fall.

Thus, any relations that might have existed between climatic temperature and the data presented in the smoothed curves for bird groups have been so obscured by periodic migratory phenomena that it has been impossible to discover any significant facts.

2. Relative Humidity Effects

A prodigious amount of work has been done on humidity in relation to the geographical distribution of birds, but little apparently on the influence of humidity on bird activities. As a factor influencing distribution, Merriam (1894) seems to regard humidity as second only to temperature in importance. Speaking of the effect on man, Milham (1923, p. 196) says: "It is the humidity, as much as the temperature, which adds to the uncomfortableness of a sultry day in summer," and a little further on, he adds, "The cold is . . . more penetrating on a damp day than on a dry day. The reason is because the moisture makes the clothing a better conductor and thus lessens the heat of the body. A moist hot day in summer is much more oppressive than a dry, hot day, because the moisture in the atmosphere prevents the free evaporation of the perspiration from the human body which cools it." Hann (1908, p. 50) cites Pettenkofer and Voit to the effect that ". . . es bringen schon Schwankungen von 1% der relative Feuchtigkeit merkliche Änderungen in der Hautausdünstung hervor." Among other effects of a low relative humidity cited by Hann are certain ones, as excitability, sleeplessness and restlessness, which would probably have an effect on activity. High relative humidity (presumably coupled with reasonably high temperature) inhibits the functions of the nervous system, resulting in restful sleep, increased carbon dioxide production, and slowed blood circulation (Hann quoting Thomas), resulting in lessened activity.

"Die relative Feuchtigkeit ist auch keineswegs eine blosse Rechnungsgrösse, sie ist ein ganz reeler klimatischer Faktor, was schon daraus hervorgeht, dass uns durch organische Substanzen direkt die relative Feuchtigkeit angegeben wird. Die organischen Substanzen sind alle mehr oder

weniger hygroskopisch und ihr Zustand, soweit er von der Luftfeuchtigkeit äbhangt, wird nicht von dem absoluten Wassergehalt der Luft, sondern von der relativen Feuchtigkeit bedingt" (Hann, 1908, p. 48).

To what extent these ideas which are based mainly on observations on men, apply to birds, is apparently not known. Probably most ornithologists are inclined to the view, expressed by Clarke (1912, p. 171) that, "It has long been realized that birds are extremely sensitive to atmospheric condi-

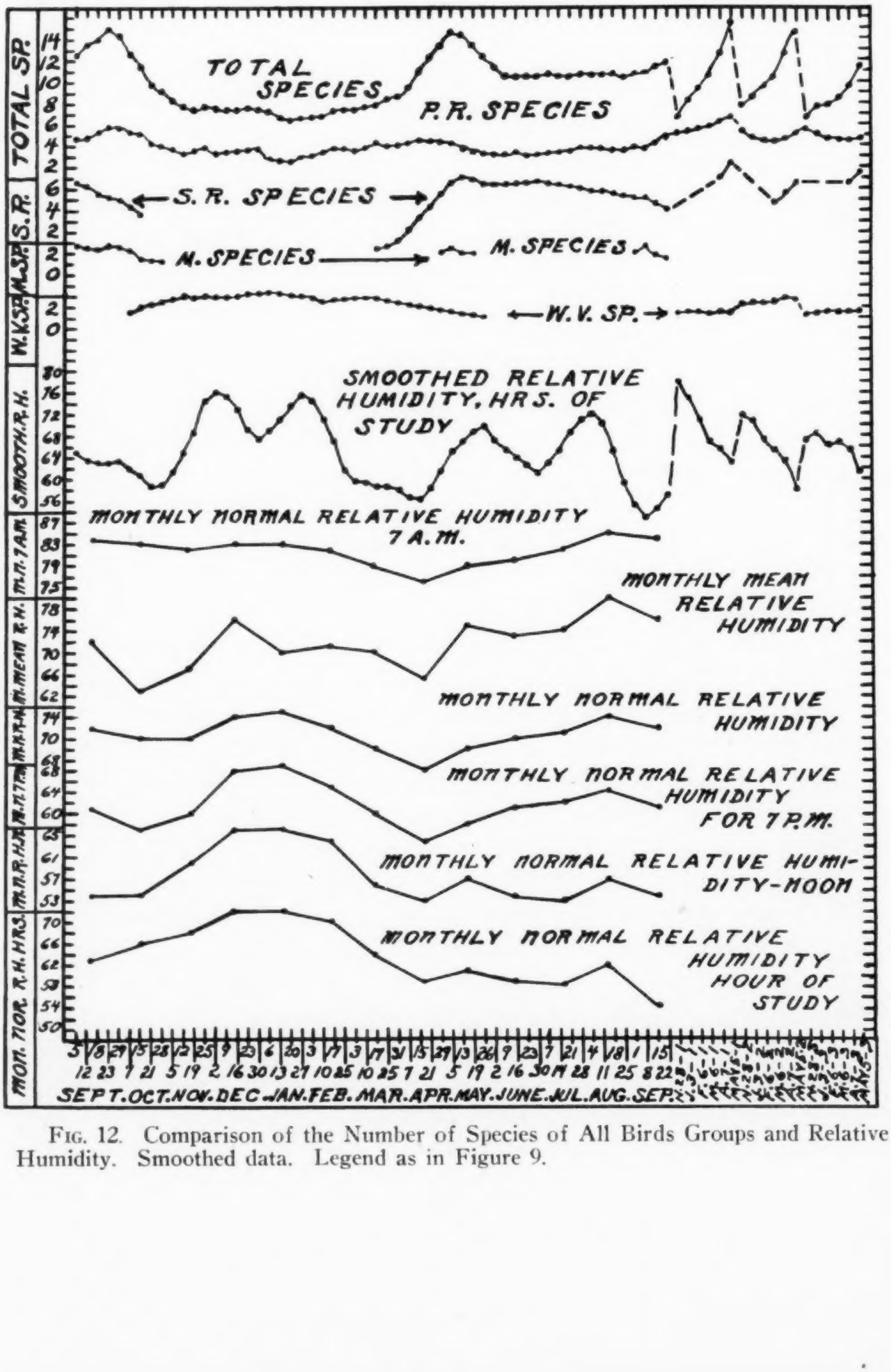

FIG. 12. Comparison of the Number of Species of All Birds Groups and Relative Humidity. Smoothed data. Legend as in Figure 9.

tions and that they discern approaching meteorological changes." To see to what extent climatic relative humidity influenced the movements of birds into and out of the depositing creek bank studied, curves of these normals were compared with the curves of the different groups of birds: (1) monthly

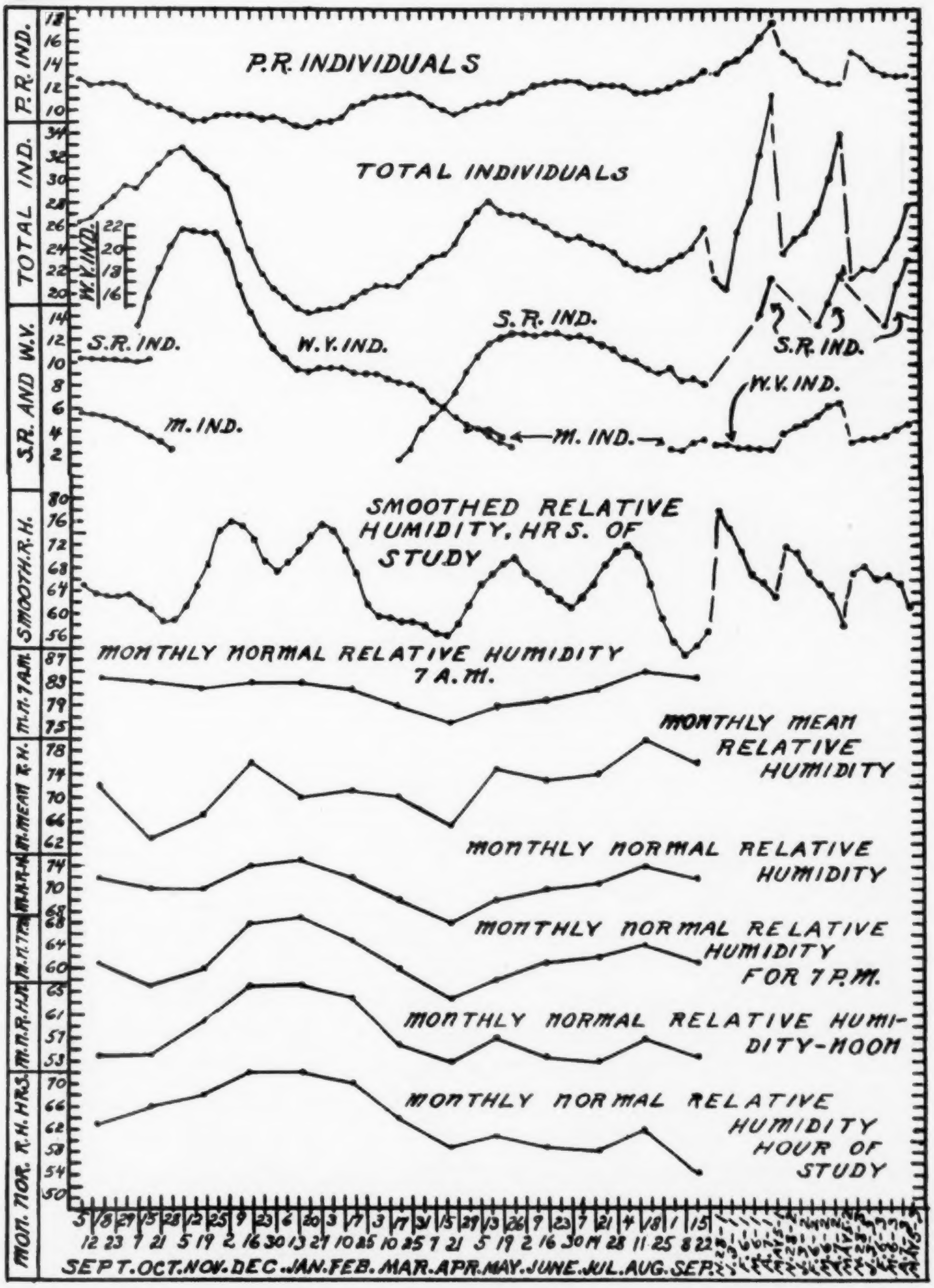

FIG. 13. Comparison of the Number of Individuals of All Bird Groups and Relative Humidity. Smoothed data. Legend as in Figure 9.

relative humidity (average of 7 a.m. and 7 p.m.), (2) monthly relative humidity for 7 a.m. (records for 35 years), (3) monthly relative humidity for 7 p.m. (records for 35 years), (4) monthly relative humidity for noon (records for six years) (Nunn, 1923). These curves are quite similar except that the one for monthly normal relative humidity for June and July is much depressed and the monthly normal relative humidity for 7 a.m. is high in October (Figs. 12 and 13). For comparison, in addition the monthly normal relative humidity for the mean hours of the field study was calculated my interpolation from the Monthly Meteorological Summary issued by the Nashville Weather Bureau. This calculation was made necessary by the fact that the local weather bureau records relative humidity for 7 a.m., noon, and 7 p.m. only. Interpolations were based on the assumption that the change in relative humidity from 7 a.m. to noon and from noon to 7 p.m. was uniform. Interpolation was to the closest five minutes. The monthly mean relative humidity curve and the nine-point-weighted smoothed curve: (formula: $\frac{a + 2b + 3c + 4d + 5e + 4f + 3g + 2h + i}{25}$) for the specific hours of the days of the field study (interpolated from the 7 a.m., and the noon and the 7 p.m. data) were also used (Figs. 12 and 13).

It may readily be seen that in their general features all of the normal relative humidity curves are quite similar. They all have a major depression in the fall (about October) and another one in the spring (about April). There are two peaks, one in midwinter and one in midsummer. Of course, the curve of normal monthly relative humidity for 7 a.m. is much flatter than the other curves due to the uniformly high relative humidity at that time of the day.

Although the curve of smoothed relative humidity for the hours of field study shows very little similarity to the other humidity curves, it represents the best measure of climatic relative humidity available that included data for each day, and so was used in this study.

It is interesting to note that migrants appeared and passed southward in the autumn with a decreasing relative humidity and that they appeared and passed northward in the spring with an increasing relative humidity. However, summer residents appeared in the spring with a decreasing relative humidity and continued to increase, even with relative humidity increasing, to a maximum in May. Then they decreased until they disappeared in the autumn in spite of the secondary maximum of relative humidity in August. Taking, as for temperature, the autumn and winter season separate from the spring and summer season, these general relations appear: The peaks of the relative humidity curves occur in midwinter at the time of the smallest number of bird species (Fig. 12) and individuals (Fig. 13) of all of the groups. This inverse relation is very slight with winter visitants (individuals) and

appears to be changed to a positive relation with winter visitant species. Permanent residents show little relation either in winter or summer. In the summer the summer residents' curve of individuals is somewhat similar to the humidity curves but the total individual curve shows little relation here. Using the method of calculating the coefficients of correlation between the smoothed relative humidity of the hours of study and the different groups of birds, the results shown in Table IX were secured.

TABLE IX. *The relation between climatic relative humidity and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Relative humidity at hr. of study.....	—0.334±0.108	0.143±0.112
P. R. Ind......	Relative humidity at hr. of study.....	—0.032±0.105	0.089±0.113
W. V. Ind......	Relative humidity at hr. of study.....	—0.053±0.112	....
S. R. Ind......	Relative humidity at hr. of study.....	....	0.381±0.097

Of these correlations, only the last one appears to be large enough, in comparison with its probable error, to be of very much significance. Yet all of the correlations in the summer period are of the same sign (plus) and may be taken as indicating a tendency for most birds to appear on the depositing creek bank in the summer when relative humidity is highest. In the winter period, all of the correlations are also of the same sign but the sign is minus and therefore opposite to the sign in the summer. This may be interpreted as indicating a tendency for birds to leave the depositing creek bank in the winter when the relative humidity is high.

3. PRECIPITATION EFFECTS

Normal rainfall is generally rather closely related to relative humidity (Hann, 1908, p. 60) and therefore, like relative humidity, may be expected to have little influence on the local movements of birds. However, neither the mean monthly precipitation for the year of the writer's study nor the normal monthly precipitation for the year of the study (Nunn, 1923) agree in all points with the normal curves of relative humidity. Accordingly, precipitation was considered separately. However, it was not possible to smooth the curves for the actual precipitation values at the hours of the field study, as was done with temperature and relative humidity, in order to get data for comparison with the bird groups because of the very erratic precipitation. Even normal precipitation gave a very saw-toothed curve.

Under these conditions, it seemed that the nine-point weighted smoothed curve of normal daily precipitation (using the same formula as was previously used for bird species) would most closely approximate climatic precipitation. Accordingly this curve has been used in the present study

along with curves of normal daily precipitation, normal monthly precipitation and average days per month with 0.01 inches or more precipitation. These precipitation curves are not very much like each other (Figs. 14 and 15). In general, normal monthly precipitation simulates the smoothed curve of normal number days per month with 0.01 inches or more of precipitation, and this last curve simulates the smoothed curve of mean monthly precipitation for 1922-1923 (with the exception of August which was the rainest August on record at Nashville. The curve of smoothed normal precipitation for days of study agrees fairly closely with the curve of mean monthly precipitation for 1922-1923 with the exception of March which was an unusually dry

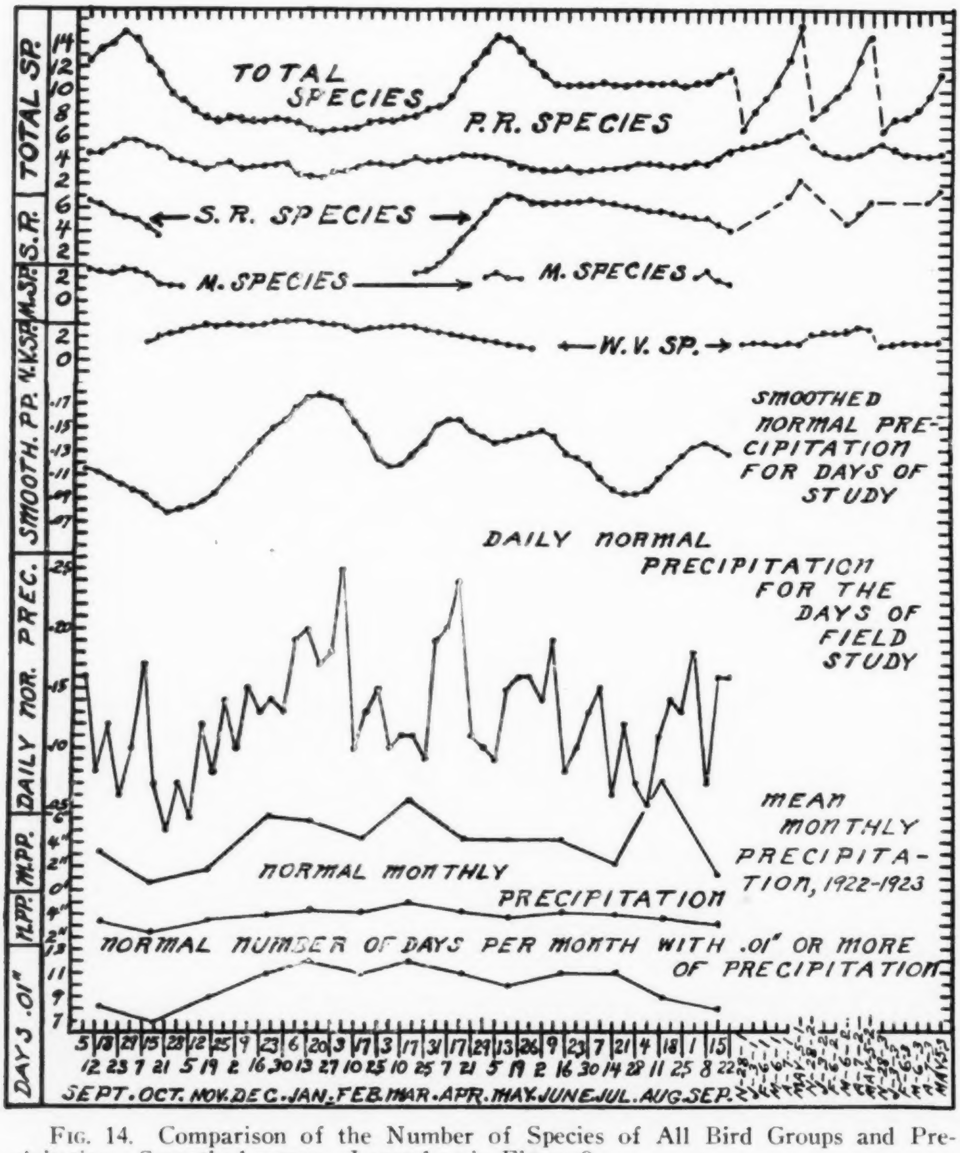

FIG. 14. Comparison of the Number of Species of All Bird Groups and Precipitation. Smoothed curves. Legend as in Figure 9.

month in 1923. When these precipitation curves are compared with the curves for bird abundance (Figs. 14 and 15), little relationship is indicated. The points of maximum precipitation neither parallel the maxima of the bird curves nor are the inverse of them. Similarly there is no relation between the minima of the precipitation curves and the minima of the bird curves. This lack of relationship is well indicated by the coefficients of correlation between

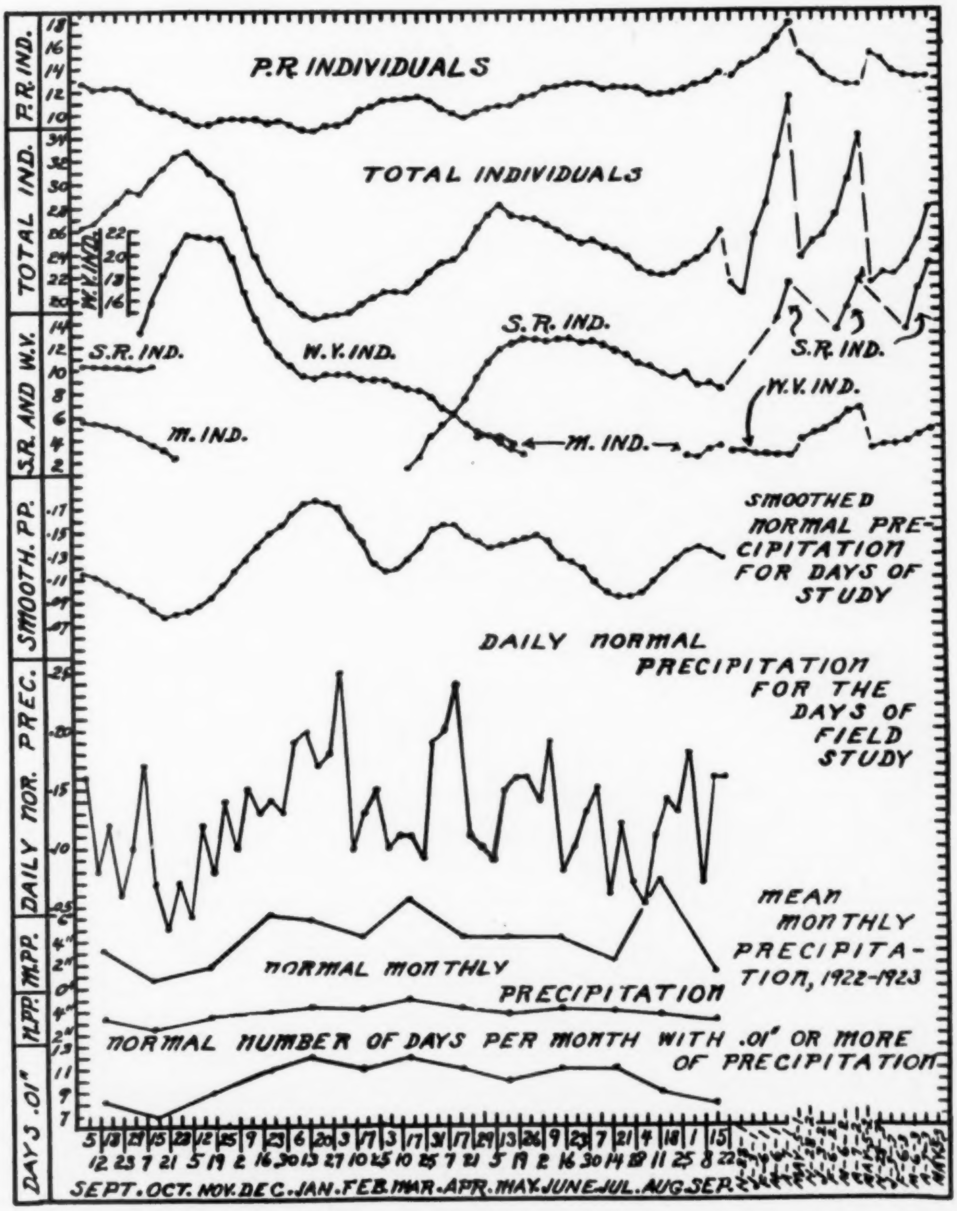

FIG. 15. Comparison of the Number of Individuals of All Bird Groups and Precipitation. Smoothed curves. Legend as in Figure 9.

numbers of individual birds and curves for smoothed normal daily precipitation for the days of the field study, as shown in Table X. It can readily be

TABLE X. *The relation between smoothed curves for normal daily precipitation and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Daily Precipitation at hr. of study.....	—0.027±0.127	—0.194±0.121
P. R. Ind......	Daily Precipitation at hr. of study.....	—0.159±0.127	—0.027±0.127
W. V. Ind......	Daily Precipitation at hr. of study.....	—0.016±0.138	....
S. R. Ind......	Daily Precipitation at hr. of study.....	....	—0.004±0.186

seen that these correlations as far too low to have any significance whatever. This may be interpreted as indicating that climatic precipitation has no effect in this area.

4. LIGHT EFFECTS

Since Garner and Allard (1920) first presented evidence showing the importance of photoperiodism in plant reproduction many investigators have believed that light may influence bird activity. The old idea of light being related to migration has been revived under the guise of a releasing stimulus to migration (Eifrig, 1924; Thomson, 1926). While the relation of light to migration as given in the earlier literature is very interesting, it will not be necessary to review it here. A good introduction to the early German papers will be found in Wach's review (1926) and to the early English literature in Schafer's (1907) paper. Light has apparently not been investigated before in relation to its probable effects on the movements of birds.

However, light appears to be related to reproduction. American poultry breeders, according to Wach (1926), have found that artificial lighting to 9 p.m., with abundant food, leads to an increase of sixteen eggs per hen per year over control hens. Recently Rowan (1925, 1926, 1927) has presented some evidence indicating that the size of the testes in juncos follows a rhythm which appears to be related to length of daylight. He considers migration as being related to this reproductive rhythm of gonad hypertrophy in the spring and atrophy in the fall. Bissonnette's work (1932) along similar lines is also interesting.

Light is also related to the activity of singing, at least, to the beginning of the morning song and the ending of the evening song, according to the investigations of Haecker (1916, 1924), Dorno (1924), and Shaver and Walker (1931). Haecker found that birds began singing earlier in the morning and sang later in the evening on sunshiny days than on cloudy days and Shaver and Gladys Walker (1930), and Shaver and Ruby Walker (1931) showed that the ending of the evening song of the robin and the mockingbird

was highly correlated with the time of sunset. Allard (1930) discovered a similar relation, although he treated his material in a different way. Shaver and Ruby Walker (1931) actually measured the light intensity and demonstrated its relationship to the ending of the evening song. Allard apparently did not measure the light intensity, but inferred a relationship between the time of beginning of the morning song and light. Although the work of these students on light does not directly relate to the numbers of birds on a small area such as the depositing creek bank, it does relate to bird activities and, in the case of migration, to movements and so might appear to be important in the present case where movements on a local scale are being considered.

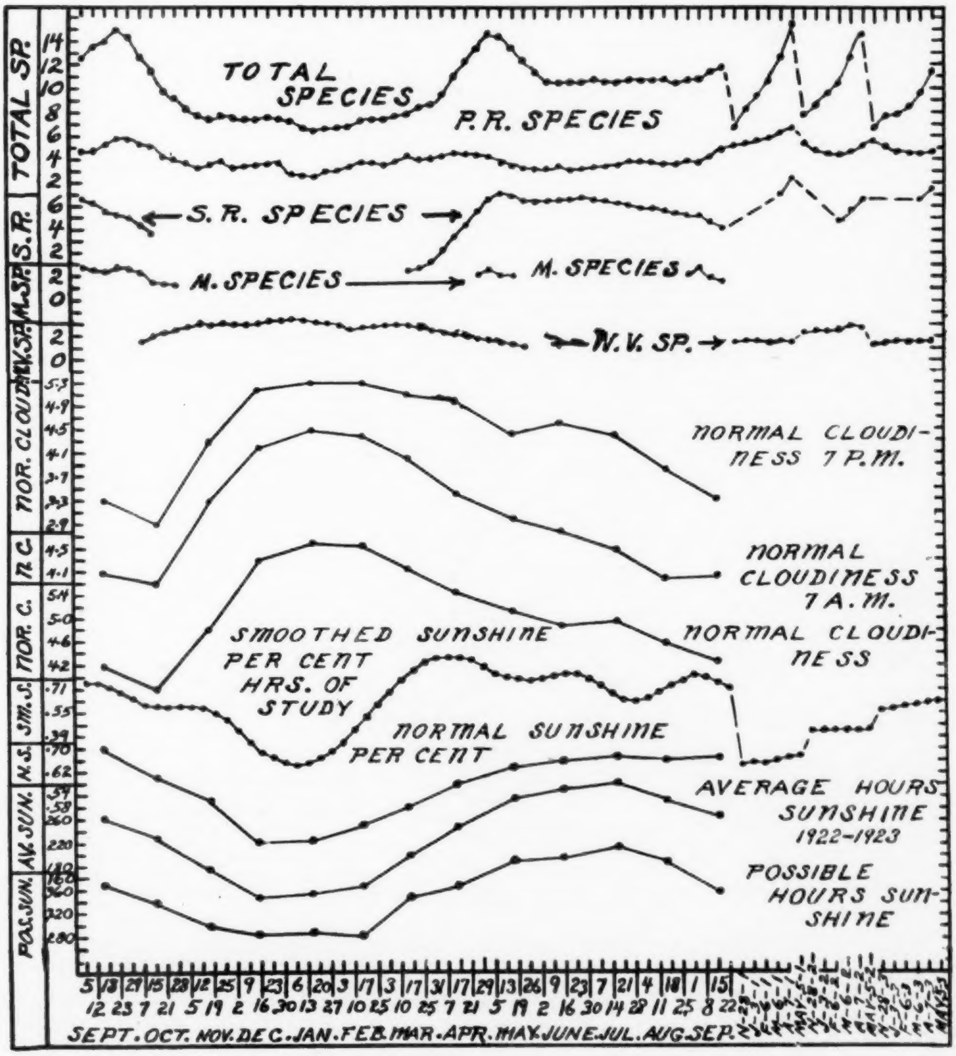

FIG. 16. Comparison of the Number of Species of All Bird Groups and Sunshine. Smoothed curves. Legend as in Figure 9.

The normal sunshine data available from the Nashville Weather Bureau (Nunn, 1923) that could be used in this analysis, were: (1) possible hours of sunshine per month, (2) average number of hours of sunshine per month (26 years), (3) per cent of possible sunshine per month (26 years), (4) monthly daylight cloudiness, scale 0-10 (34 years) for 7 a.m., and (6) the same for 7 p.m. (40 years). These were taken as indicating the general climatic sunshine conditions of the Nashville region. In addition, since normal hourly sunshine conditions were not available, a smoothed curve was constructed to show the percentage of possible sunshine for the hours of the field

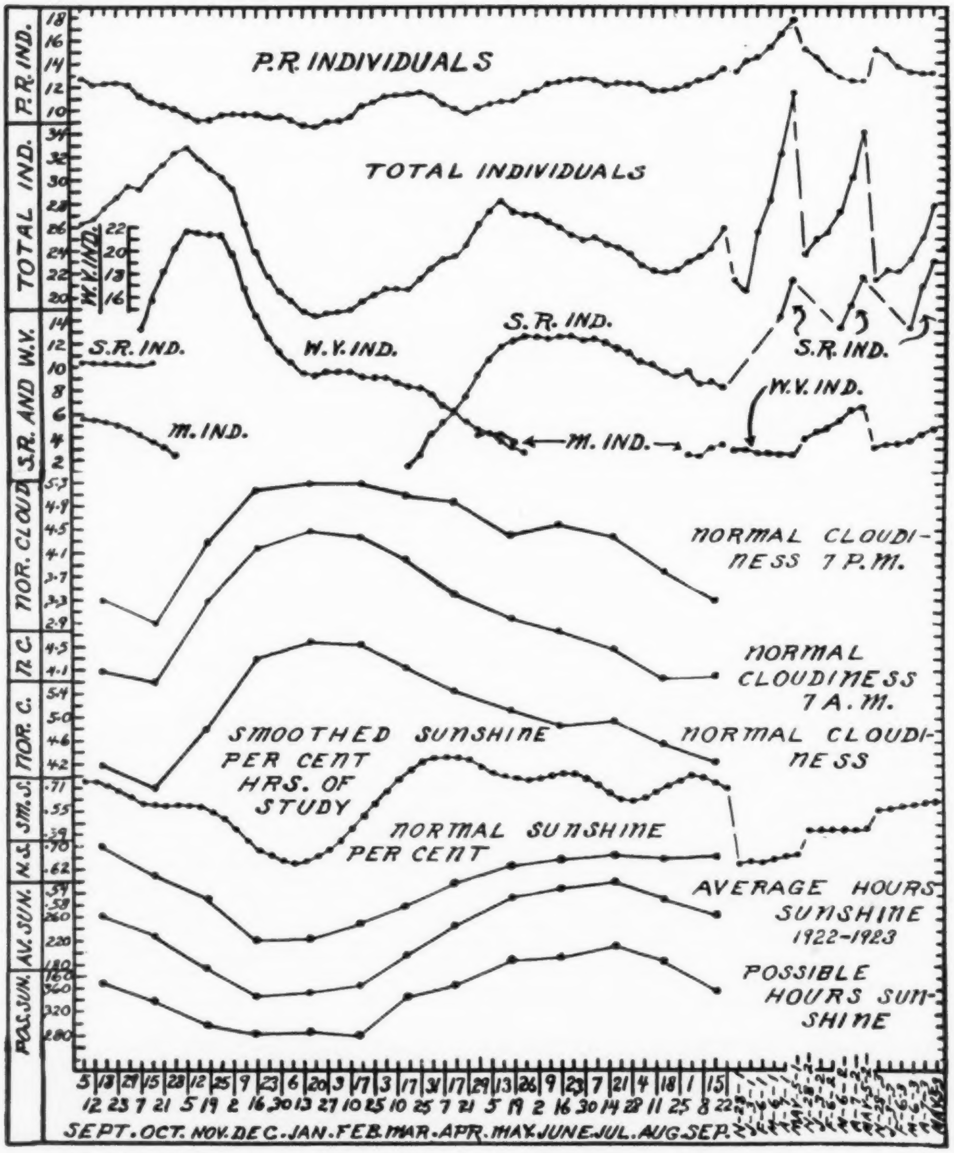

Fig. 17. Comparison of the Number of Individuals of All Bird Groups and Sunshine. Smoothed curves. Legend as in Figure 9.

study (interpolated to within three minutes and then smoothed by the nine-point weighted formula previously used in this paper and then smoothed a second time by this same formula. It was expected that this curve would approach climatic sunshine conditions. It is very similar to the curve of percentage of possible monthly sunshine except that the smoothed curve is very high in March, April, and May and low in July (Fig. 16). The curves of cloudiness are of course approximately the inverse of those of sunshine.

A comparison of these seven sunshine curves with the curves for bird abundance (Figs. 16 and 17) indicates only a very general relation between some of the curves. With decreasing light in the autumn, migrants appeared and later disappeared, summer residents disappeared, permanent residents persisted without any great change, and winter visitors appeared, increased to a maximum in November and then gradually decreased in numbers. In the spring with increasing light, the winter visitors continued to decrease and finally disappeared (with average monthly light and the smoothed curve of light at the hour of the study decreasing), migrants appeared and later dis-

TABLE XI. *The relation between climatic sunshine and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Sunshine duration at hr. of study......	0.034±0.108	—0.072±0.113
P. R. Ind......	Sunshine duration at hr. of study......	0.246±0.101	—0.087±0.113
W. V. Ind......	Sunshine duration at hr. of study......	0.024±0.112	....
S. R. Ind......	Sunshine duration at hr. of study......	....	—0.072±0.113

appeared, and summer residents appeared, reached a maximum with the light maximum and then gradually decreased with the decreasing light throughout the summer. Thus summer residents seem to be more closely related to light in their movements than any other group. It should be noted that in the late autumn and early winter with an increase of cloudiness, there is a general decrease of sunshine and in the late winter and early spring, a decrease in cloudiness is accompanied by an increase in sunshine. However, in the late summer and early autumn, there is a decrease in cloudiness accompanied by a decrease in hours of sunshine (but not in percentage of possible sunshine). In general, then, there appears to be little relation between the different curves showing abundance of bird groups and the curves of sunshine. This lack of relationship is borne out by the coefficients of correlation (Table XI) which are all low.

5. WIND EFFECTS

Although it has been known for a long time that gulls tend to fly against the wind and thus collect in the lea of islands or even pass inland a considerable distance from water, there appears to be little data in the literature on

local movements of land birds influenced by wind. Some of the European investigators (for example, Haecker, 1916) held to the old view that wind was very important, especially the "fohn" wind in spring migration. However, Eagle Clarke's work (1896, 1912) indicated that winds in themselves were unimportant as regards direction and velocity, unless the wind was so strong that it acted as a barrier to migration, blew birds out of their course, or, if they were overtaken at sea, caused them to arrive exhausted or to perish in immense numbers. The apparent relation of winds to migration is due to the fact that winds frequently accompany conditions of barometric pressure which are favorable to migration. Thus when the wind is from the south or southeast, there is the greatest movement of birds between the British Isles and the continent both in autumn and spring because the high pressure area is to the south or southeast of the British Isles. A northwest wind is most unfavorable because the high pressure area is to the north or north-

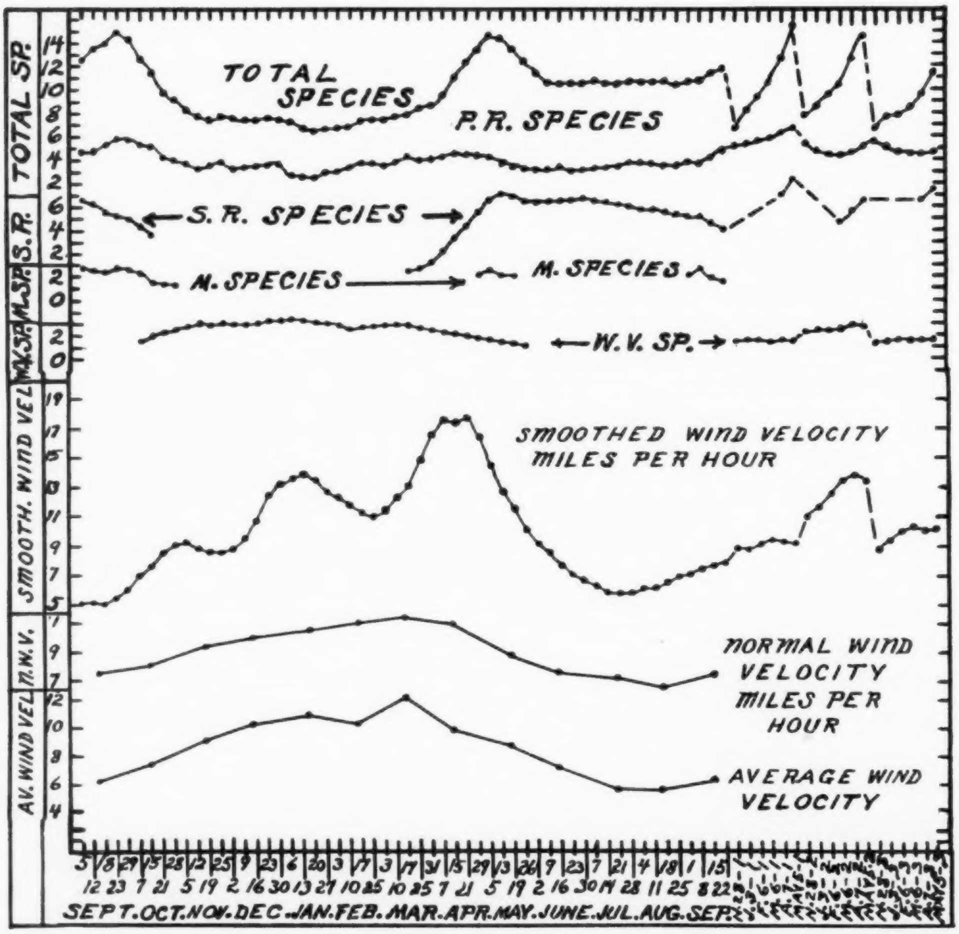

FIG. 18. Comparison of the Number of Species of All Bird Groups and Wind Velocity. Smoothed curves. Legend as in Figure 9.

west. Clark thinks that it is the position of the barometric pressure areas that is primary; winds are secondary. Towbridge (1902) found that all of the great autumnal flights of hawks near his home were made when the wind was north or northwest and when its velocity was high (20 miles per hour or more).

The wind data from the Nashville Weather Bureau included the average monthly velocity in miles per hour and the normal monthly wind velocity. Normal wind velocities for the period of study were calculated by interpolation from the normal hourly wind velocities. Curves for these velocities were smoothed by the nine-point-weighted method previously used and then these curves were compared with the curves of birds (Figs. 18 and 19).

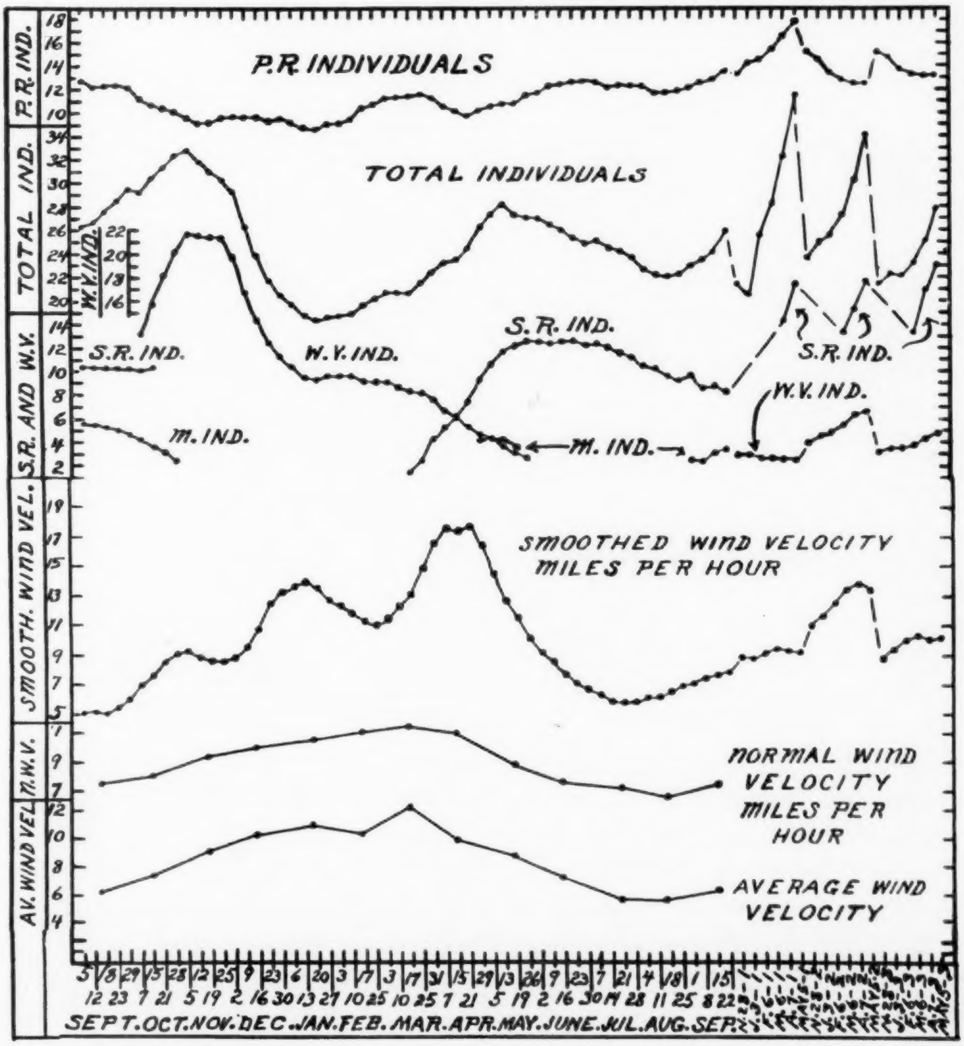

FIG. 19. Comparison of the Number of Individuals of All Bird Groups and Wind Velocity. Smoothed curves. Legend as in Figure 9.

It is very difficult from a comparison of the curves to see any relationship whatever between the numbers of birds and the velocity of the wind. The coefficients of correlation likewise are low (Table 12) with the exception of total individual birds and wind velocity during the winter. Here the relation is a negative one but significantly high. It apparently means that there were more birds on the depositing creek bank when the average wind velocity was low and fewer when the wind was high in the winter. It should be noted that all of the correlation coefficients are negative (with the exception of total individuals in the summer with a coefficient too low to be significant). While most of these coefficients are low, they may be taken as indicating a tendency for there to be more birds in this area when there is less wind. This may reflect in part the effect of the wind on the observer. Birds are more difficult to find on a windy day: they sing little on such a day, and they cannot be

TABLE XII. *The relation between climatic wind velocity and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Wind velocity at hr. of study.........	—0.700±0.055	0.082±0.113
P. R. Ind......	Wind velocity at hr. of study.........	—0.206±0.103	—0.290±0.104
W. V. Ind......	Wind velocity at hr. of study.........	—0.342±0.099	....
S. R. Ind......	Wind velocity at hr. of study.........	....	— .282±0.105

TABLE XIII. *Wind directions for the periods of the field work.*

WIND	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Normal prevailing wind (50 year's record).........	E	NE	S	NE	S	NW	S	S	E	S	NE	SW	NW
Average prevailing wind, hours of study..........	NE	NE	S	NE	S	NW	NW	S	E	SE	W	SW	NW
Monthly prevailing wind, Sept. 1922 to Oct. 1932....	NW	NW	NW	S	NW	NW	S	S	NW	SW	SW	SW	NW

located by a swaying twig. However, the observer took great care to be as accurate as possible. He is inclined to think that the birds were elsewhere rather than on this particular creek bank when the wind velocity was high.

The only relations which appear in comparing bird numbers with wind directions are these: The spring maxima of total species and individuals of birds occurred when the prevailing wind for the hours of study and for the month was from the east, the autumn maxima when the prevailing wind was from the south. The minima of total species and individuals occurred with a normal prevailing wind from the northwest, a monthly prevailing wind and the mean prevailing wind for the hours of study from the south. The sum-

mer minima for total species and number of individual birds occurred with the prevailing wind from the southwest. Thus it seems hardly likely that prevailing wind direction is of any very great moment in the local movements of birds.

6. ATMOSPHERIC PRESSURE

Ordinary changes in atmospheric pressure have no direct effect on organisms, according to Hann (1908, p. 76). The daily changes in pressure are small, seldom as much as 22 mm. However, Clark (1896, 1912) ascribes to the location of the anticyclonic areas a very great importance in migration. He says that all of the great movements of birds between the British Isles and the continent, both in autumn and spring, occur when there is an anticyclone over northwestern Europe and a gentle gradient extending beyond the shores of the British Isles. Following the clue given by Clark's work, the

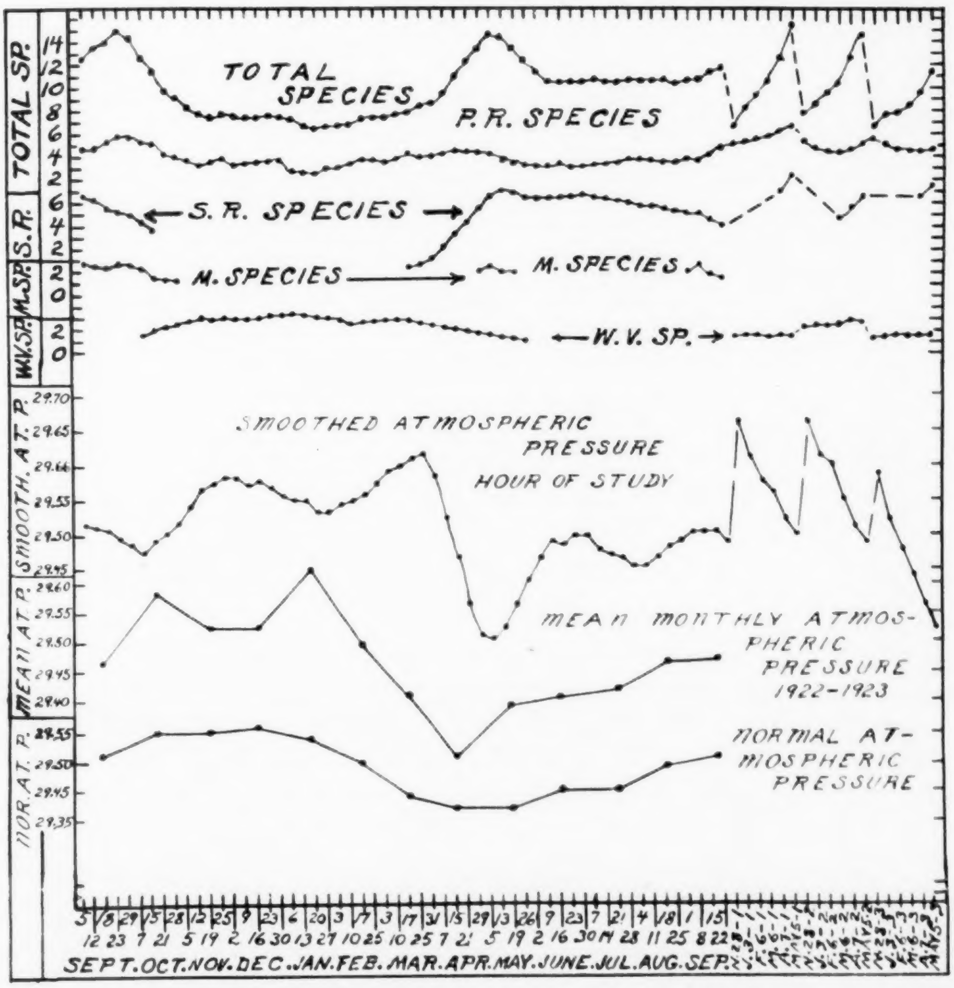

FIG. 20. Comparison of the Number of Species of All Bird Groups and Atmospheric Pressure. Smoothed curves. Legend as in Figure 9.

monthly normal atmospheric pressure for Nashville, the average monthly atmospheric pressure for the months of the study, and the smoothed curve of atmospheric pressure for the hours of the study, were plotted with the bird curves (Figs. 20 and 21).

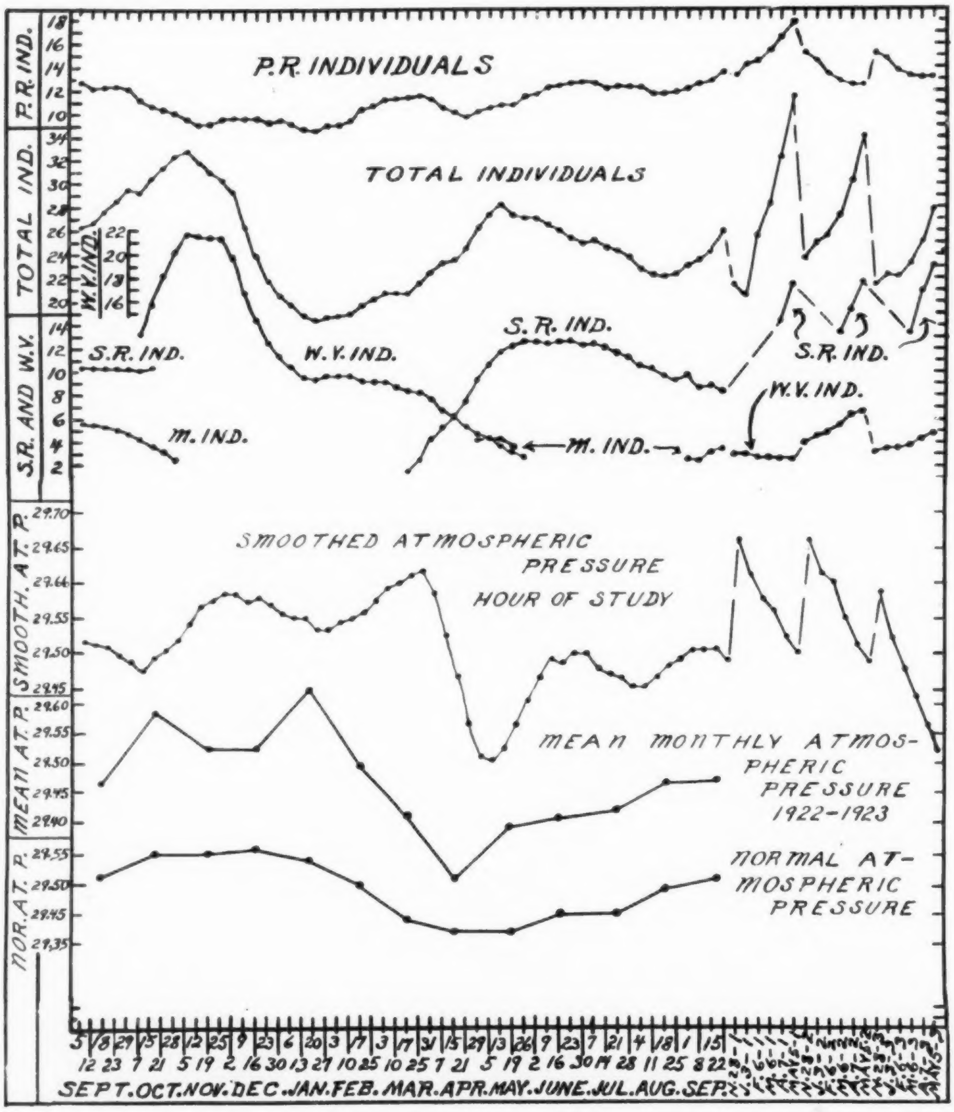

FIG. 21. Comparison of the Number of Individuals of All Bird Groups and Atmospheric Pressure. Smoothed curves. Legend as in Figure 9.

These curves when compared indicate little relation between atmospheric pressure and the number of birds in this area. This apparent lack of relation is confirmed by the coefficients of correlation (Table 13); all of which are low—too low, it appears, to have much significance. The highest of these for the winter half-year is -0.295 ± 0.099. This is the coefficient of corre-

lation between smoothed atmospheric pressure and smoothed number of birds. It indicates a tendency for all birds to be fewer when the atmospheric pressure is highest. The same tendency is indicated for the summer half-year by the correlation coefficient (-0.380 ± 0.066) of summer resident birds and atmospheric pressure, but the opposite tendency appears to be indicated by the coefficient for permanent resident birds.

TAPLE XIV. *The relation between climatic atmospheric pressure and smoothed bird groups.*

Bird Group	Climatic Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Atmospheric pressure at hr. of study...	—0.295±0.099	—0.160±0.111
P. R. Ind......	Atmospheric pressure at hr. of study...	0.011±0.108	0.241±0.107
W. V. Ind......	Atmospheric pressure at hr. of study...	—0.114±0.111	....
S. R. Ind......	Atmospheric pressure at hr. of study...	....	—0.380±0.066

7. SUMMARY AND DISCUSSION OF THE RELATION OF CLIMATE TO BIRD NUMBERS

As the result of preliminary treatment of the data collected, it seemed most significant to consider the winter half-year (September 21-March 21) separate from the summer half-year (March 21-September 21). While the study involved a comparison of the different bird groups both graphically and statistically, the statistical method lends itself best to summarization. Accordingly, each bird group will be considered separately in regard to its coefficients of correlation with the various climatic factors, by season.

WINTER SEASON (SEPTEMBER 21-MARCH 21)

Total Individuals (Smoothed Curves). All of the birds were related to climatic factors in the following order:

(1) Wind velocity ($r = -0.700 \pm 0.055$)
(2) Temperature ($r = 0.674 \pm 0.059$)
(3) Relative Humidity ($r = -0.344 \pm 0.108$)
(4) Atmospheric Pressure ($r = -0.295 \pm 0.099$)
(5) Sunshine Duration ($r = 0.034 \pm 0.108$)
(6) Precipitation ($r = -0.027 \pm 0.127$)

The first two factors (wind and temperature) certainly show a significantly high correlation with climatic factors. The higher the wind on the average, the fewer birds, but the higher the temperature, the greater the number of birds. The other climatic factors do not appear to be significant enough to be singled out for emphasis.

Permanent Residents (Smoothed Curves). Unlike the group just considered, permanent resident individuals (smoothed) are very conservative and

show little relation to any climatic factor. Perhaps this is what should be expected of a group of this kind. The highest correlation is with temperature (r = -0.247 ± 0.107). It should be noted that the relation is opposite in sign to that of temperature with total birds. This suggests that the colder the weather the larger the number of permanent resident birds on the creek bank studied. This was what was expected of all birds before the study was started, since the creek bank is in front of a south-facing slope and so would be a locally warmer area in winter. Doubtless migrants and summer residents during the early fall and late spring have caused the large positive correlation for total birds.

Of the other correlations with permanent residents, light is high enough (0.246 ± 0.101) to deserve some comment. The relation is positive, the more light, the more birds. This falls in line with the temperature relations, since bright days are usually cool during the winter, and cloudy or rainy days, warm.

For comparison, all of the correlations of permanent resident birds and climatic factors are given below in order.

(1) Temperature (r = -0.247 ± 0.107)
(2) Sunshine Duration (r = 0.246 ± 0.101)
(3) Wind Velocity (r = -0.206 ± 0.106)
(4) Precipitation (r = -0.159 ± 0.127)
(5) Relative Humidity (r = -0.032 ± 0.105)
(6) Atmospheric Pressure (r = 0.011 ± 0.108)

Winter Residents (Smoothed Curves). Winter residents during the season from September 21 to March 21 were significantly correlated only with temperature (r = 0.554 ± 0.078) and wind velocity (r = -0.342 ± 0.099). This indicates that most individuals of this group were present in this habitat (depositing creek bank) in the fall and in the spring, when the temperature was highest. This agrees well with observations for the whole Nashville region and probably means that most of the individuals of winter residents are actually migrants passing to a winter home farther south in the autumn and to their summer home farther north in the spring.

The greatest movement of individuals is in the autumn season when the wind velocity is lowest and this is the reason for the negative correlation with wind.

Although the other coefficients of correlation are small, they are here given for the sake of completeness:

(1) Temperature (r = 0.554 ± 0.078)
(2) Wind Velocity (r = -0.342 ± 0.099)
(3) Atmospheric Pressure (r = -0.114 ± 0.111)
(4) Relative Humidity (r = 0.053 ± 0.112)

(5) Sunshine Duration ($r = 0.024 \pm 0.112$)
(6) Precipitation ($r = -0.016 \pm 0.138$)

SUMMER SEASON (MARCH 21-SEPTEMBER 21)

Total Individuals (Smoothed Curves). During this season, this group of birds was related to climatic factors (as shown by coefficients of correlation) in the following order:

(1) Temperature ($r = -0.409 \pm 0.095$)
(2) Precipitation ($r = -0.194 \pm 0.121$)
(3) Atmospheric Pressure ($r = -0.160 \pm 0.111$)
(4) Relative Humidity ($r = 0.143 \pm 0.112$)
(5) Wind Velocity ($r = 0.082 \pm 0.113$)
(6) Sunshine Duration ($r = -0.072 \pm 0.113$)

Of these correlations, only the one with temperature is large enough to be significant. It indicates that the most birds are on the depositing creek bank when the temperature is coolest, namely in the spring and fall. In this respect the creek bank studied seems similar to the Nashville region as a whole.

Permanent Residents (Smoothed Curves). All of the coefficients of correlation of climatic factors with this group of birds are very low, thus indicating again the relative conservatism of the group. Although probably none of these coefficients are high enough to be considered significant, they are here summarized for completeness.

(1) Wind Velocity ($r = -0.290 \pm 0.104$)
(2) Temperature ($r = -0.247 \pm 0.107$)
(3) Atmospheric Pressure ($r = 0.241 \pm 0.107$)
(4) Relative Humidity ($r = 0.089 \pm 0.113$)
(5) Sunshine Duration ($r = -0.087 \pm 0.113$)
(6) Precipitation ($r = -0.027 \pm 0.127$)

Summer Residents (Smoothed Curves). The order of the relation between this group of birds and climatic factors is as follows:

(1) Relative Humidity ($r = 0.381 \pm 0.097$)
(2) Atmospheric Pressure ($r = -0.380 \pm 0.066$)
(3) Wind Velocity ($r = -0.282 \pm 0.105$)
(4) Sunshine Duration ($r = -0.072 \pm 0.113$)
(5) Temperature ($r = 0.008 \pm 0.114$)
(6) Precipitation ($r = 0.004 \pm 0.186$)

The surprising thing about this order is the relatively high rank of relative humidity and the low position of temperature. This is in marked contrast to their relations in the other groups of birds.

VII. THE EFFECT OF WEATHER INFLUENCES UPON THE BIRD POPULATION OF THE DEPOSITING CREEK BANK

In the preceding section, the relation between climatic factors and number of birds present on the depositing creek bank was analyzed. Smoothed weather factors were used mainly since they were found to approximate closely climatic factors, and smoothed number of birds in order to make the data comparable. If then smoothed weather factors represent the slow, gradual seasonal changes, which are called climate—practically free from the daily fluctuations making up weather—the daily deviations from these smoothed curves ought to represent weather factors free from the influence of climate. Likewise the deviations of bird numbers from the smoothed curves of bird abundance ought to be comparable with the deviations of weather factors from climatic factors. Accordingly, in this analysis of weather effects, the deviations of the different groups of birds from their smoothed curves are compared with the deviations of the different weather factors from corresponding climatic factors. These weather factors are considered one at a time in the same sequence as was used in the section on climatic effects.

1. Temperature Effects

As to local movements of birds in winter, Wachs (1926) cites Faber's (1826) study of birds of the far north to the effect that the birds react in one of three ways: (1) they pass from the north to the southern part of the island, (2) they collect at the very end of a narrow bay, or (3) they concentrate in the settlements (Siedlungen). Some of the birds which collect in the settlements are migratory in other regions. Examples are the Oystercatcher (*Haematopus ostralegus* L.), the Water Rail (*Rallus aquaticus* L.), and the Starling. Clark (1896) says of winter movements southward, that they are entirely due to a decided fall in temperature, usually with frosts and snows. These movements become more pronounced as winter advances and especially in severe seasons. They are repeated during each cold spell in the months of December, January, February, and in some exceptional seasons as late as the third week of March (in the British Isles).

After migration has taken place in the spring, a sharp cold spell may cause a retrograde movement, as apparently happened in the Connecticut Valley with robins, bluebirds, blackbirds, song sparrows, fox sparrows, and many other species in the spring of 1925 (Bagg, 1925). Haecker (1916) mentions a similar retrograde movement of birds from a mountain to a valley 1,200 meters lower, following a snowstorm. He thinks that an analysis of situations such as these will solve the problem of the influence of weather on migration. Deane (1895) mentions a great collection of birds in the large open space around a 60,000 gallon-per-day artesian spring in Texas during the heavy snowstorm of February, 1895. It may be that the habit of the white-

crowned sparrow in Colorado (Antony, 1891) of raising their two breeds at different altitudes is also related to temperature.

Then the number and kinds of birds in a local area may be influenced by temperature, especially by unusually low temperature, through its destructive action on bird life. Barrows (1906) speaks of the great destruction of birds on Lake Michigan in September, 1897; and Roberts (1907) of the loss of life of Lapland longspurs in Minnesota in March following a soft, wet snow. He counted five and one half birds to 400 square feet, which equaled 750,000 birds for the two lakes, and estimated the total loss around Slayton to be 1,500,000 birds. Similar reports have been made for other sections of the country by Attwater (1892), Deane (1914), Saunders (1907), and many others.

That such accidents have a real effect on the summer bird life is indicated by the work of several observers. Barrows (1906) says that it took the robins six years to regain their normal numbers after the severe winter of 1894-1895. After the severe summer of 1903 and the winter of 1903-1904, Forbush (1905) found bobwhites almost exterminated, ruffed grouse and chimney swifts much reduced in numers, purple martins rare, and practically all other groups of birds much reduced in numbers.

Porter (1908) reports very late nesting of warblers, vireos, the towhee and the blackcap chickadee in 1907 due to the cold spring. In many cases, there was quite a delay between the laying of the first egg and the completion of the set. For this same spring (Eifrig, 1908) describes the migration as much drawn out.

It is necessary to call attention again to the very definite work of Clarke (1896, 1912) on migration. His data indicate quite conclusively that a rise of temperature in winter when migrants are in a certain physiological condition, sends them northward. In the autumn, a drop in temperature sends them southward. This has been later confirmed by Cooke (1913b) and by Smith (1917).

Shaver and Walker (1930) found an activity of the eastern mockingbird, *viz.*, the time from sunset that this bird stopped singing, related in part to temperature. The coefficient of correlation was 0.57 ± 0.07. This indicates that the eastern mockingbird stops his evening song later on warm days and earlier on cooler evenings.

All of the observations and analyses (except Bretscher's) reviewed indicate the very great importance of temperature fluctuations in bird activities.

In this study, there seemed to be little relation (Fig. 22) between temperature and the number of species of birds present. The peaks of temperature do not correspond to the peaks of the bird curves nor *vice versa*. No other significant relationships appear.

The curves based on number of individual birds (Fig. 23) are considered in detail because they really represent the curves of species weighted and have larger numbers so that they are better fitted for statistical treatment. At first the seventeen peaks of the total bird curve were compared with the temperature deviation curve. On six of these peaks, the temperature was below that of the smoothed curve, on three the same as the smoothed value, and on eight higher than the smoothed curve. This division was not seasonal.

Likewise the sixteen large depressions in the total bird curve were com-

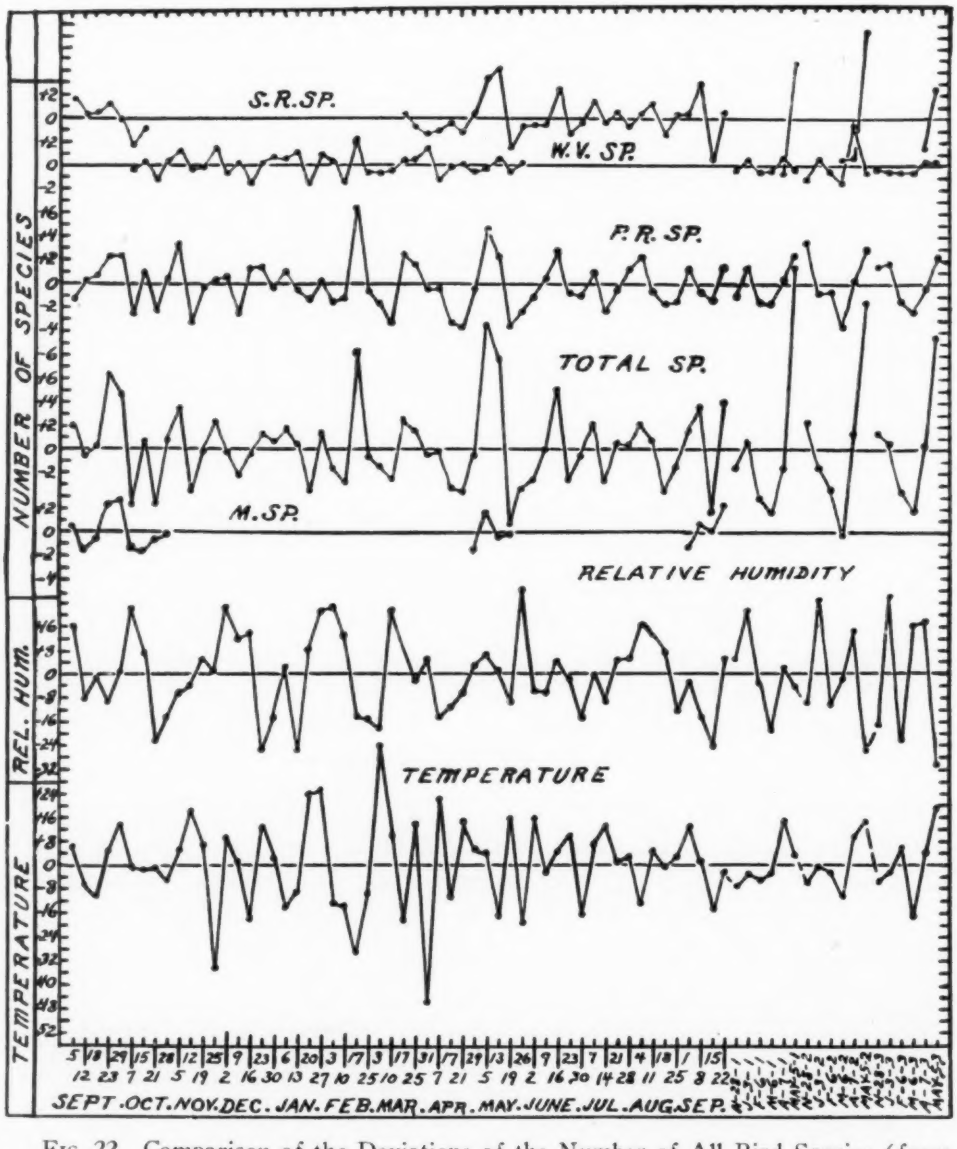

FIG. 22. Comparison of the Deviations of the Number of All Bird Species (from their Smoothed Values) and Temperature and Relative Humidity Deviations (from their Smoothed Values). Legend as in Figure 9.

pared in the same manner with the temperature deviations for the same periods. Nine of these occurred when the temperature was lower than its smoothed value and seven when the temperature was higher. These depressions are seasonally distributed, for in the southward-moving period, the temperature deviations were minus in seven cases and plus in only two; in

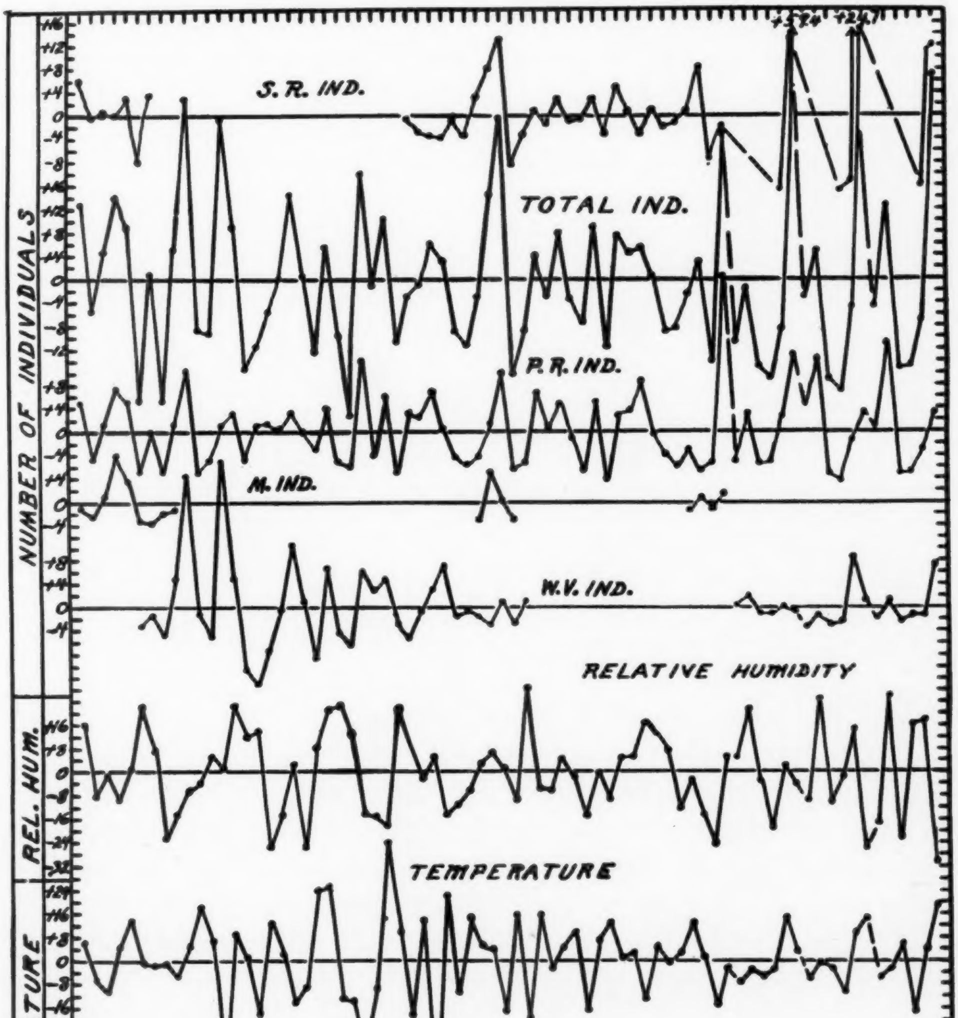

FIG. 23. Comparison of the Deviations of the Number of Bird Individuals (from their Smoothed Values) and Temperature and Relative Humidity Deviations (from their Smoothed Values). Legend as in Figure 9.

the northward-moving period, they were plus in five cases and minus in only two. This suggests that some date near midsummer and some date near midwinter would separate the data into that showing a plus correlation with temperature in the fall and a minus correlation in the spring. This suggestion was checked by comparing the curves of total birds and temperature from June 20 to December 21 and from December 21 to June 21, but no relation was found; approximately half of the points on the two curves were of the same sign (either plus or minus) and half of the opposite sign, for each period. The coefficients of correlation for these periods similarly were very low.

Experiments with other time division points likewise yielded unsatisfactory results. Finally the equinoxes were selected as division points because they were the division points in the climatic analyses. First, each curve of the bird groups was compared with the temperature curve point by point for each period of time (September 21 to March 21 and March 21 to September 21). Since little relation appeared here from this method of study, coefficients of correlation were tried. The values obtained are shown in Table XV.

TABLE XV. *The relation between temperature deviations (from smoothed curves) and bird deviations (from smoothed curves).*

Bird Group	Weather Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Temperature deviations at hr. of study	0.062 ± 0.108	0.243 ± 0.107
P. R. Ind......	Temperature deviations at hr. of study	0.023 ± 0.108	-0.003 ± 0.114
W. V. Ind......	Temperature deviations at hr. of study	-0.081 ± 0.113	....
S. R. Ind......	Temperature deviations at hr. of study	....	0.143 ± 0.112

These results apparently indicate very little relationship between temperature fluctuations and the presence of birds on the depositing creek bank. This was a great surprise to the writer for he previously had felt that this protected creek bank (Fig. 1) would be a great rendezvous for birds on the cold days of winter, because the hills to the north and west would act as windbreaks against cold winds, and on the really hot days of summer because of the shade and the creek. The low correlation with permanent residents was expected for even with climatic seasonal changes they have been found very conservative. The smallness of the summer correlations with temperature may be due to the fact that most of the field studies were made between 9 and 10 a.m., long before the hot part of the day was reached.

Taking the clue from Clark's (1896, 1912) work on migration, that it is not the absolute temperature that is important but the change in temperature from that of the preceding day, the direction of the change of mean temperatures was indicated for each day of the study. When the direction of

change in temperature from that of the last field trip was compared with the direction of change of bird numbers, no relation appeared. During the spring and summer period, there were thirteen times when either an increase in temperature was accompanied by an increase in total birds or a decrease in temperature with a decrease in birds, and fifteen times when the opposite result took place. The fall and winter period gave twelve times alike and fifteen unlike for total birds. Thus there seemed to be little relation between either the daily temperature fluctuations or the direction of temperature change from that of the preceding trip and the numbers of birds on the depositing creek bank.

2. Humidity Relations

The deviations from the smoothed curves of birds (individuals) were compared with the deviations of relative humidity from its smoothed curve in a very similar manner to that employed in studying temperature (Figs. 22 and 23). Curve comparisons yielded no worthwhile data and so coefficients of correlation were calculated. The coefficients of correlation of relative humidity deviations and deviations of the different bird groups are given in Table XVI.

TABLE XVI. *The relation between relative humidity deviations (from smoothed curves) and bird deviations (from smoothed curves).*

Bird Group	Weather Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind.	Daily fluctuations at hr. of study	0.006±0.114	—0.253±0.107
P. R. Ind.	Daily fluctuations at hr. of study	0.108±0.113	0.053±0.114
W. V. Ind.	Daily fluctuations at hr. of study	—0.097±0.113	....
S. R. Ind.	Daily fluctuations at hr. of study	....	—0.364±0.099

Thus there appears here no relation between the daily fluctuations of relative humidity in the fall and winter period and the daily fluctuations of birds. This is also largely true in the spring and summer period in spite of the minus correlation of 0.253 with total individuals and 0.364 with summer residents, because of the high probable error. At most these data indicate a slight tendency to leave the creek bank in the summer when the relative humidity is high and to collect on the creek bank when the relative humidity is low. This absence of relationship between relative humidity and the presence of birds on the depositing creek bank is very similar to the results obtained by Elliott (1932) in a study of the relation of relative humidity to the time of ending of the evening song of ten common birds. He found correlation coefficients that varied from -0.001 ± 0.06 for the southern robin to -0.34 ± 0.07 for the house sparrow, and from 0.005 ± 0.06 for the eastern mockingbird to 0.30 ± 0.08 for the Carolina wren.

3. PRECIPITATION INFLUENCES

The data on precipitation is quite inadequate for yielding worthwhile results. On only four trips (January 20, 1923, .03"; May 26, 1923, .10"; August 4, 1923, .19"; and January 3, 1926, 1st trip, .12") of the seventy-four was there as much as .01" of rain during the hours of data collection. There was a trace on seven additional days, distributed as follows: December 2 and 16, 1922; January 27, March 10, and July 14, 1923, and January 3 (3rd trip) and April 7 (2nd trip), 1926. All of these trips have a minus deviation of total bird individuals (with the exception of the April, 1926, trip) which is especially marked on those four trips having more than 0.01" of rainfall during the hour of study. This relation may be more apparent than real for field observation indicates that birds usually hide themselves in protected places and become very quiet during a rain. This would make them difficult to find and this difficulty might be further increased by poor visibility.

4. WIND AND BIRD NUMBERS

As previously mentioned, Clark (1896, 1912) found that wind, unless accompanied by certain barometric relations, was of no importance in migration. However, if it is strong, it acts as a barrier. Alford (1925) found that wind was the most important factor, temperature the least, in influencing the length of time that the song thrush sings after sundown (based on three year's daily records from February 1 to June 10). Force of wind was very important but his graph (page 310) shows fairly strong winds varying from eleven to thirty-six miles per hour. Haecker (1916, 1924) secured negative results between force of wind and the time that birds sing after sunset but he was dealing with all strengths of wind and many kinds of birds. Alford (1925) found direction of wind next to wind force the most important factor in the song of the song thrush. For East Anglia, his Table B (p. 309) indicates that the song period is most prolonged when the wind is from the northeast, west, or southwest. Again Haecker's data (1916) for Alsace-Loraine and Switzerland with several kinds of birds, indicate no relation. With man, wind decreases the influence of high humidity when the temperature is high and also when temperature is low.

When the data in this study are plotted (Figs. 24 and 25) they indicate no apparent relation between wind velocity and number of bird species or individuals. Similarly, when the wind velocity deviations were correlated with the bird deviations (Table XVII), no very significant relations were found.

All of these correlations are low and cannot be regarded as indicating much relation to wind velocity. Such relationship as is shown suggests that birds leave the depositing creek bank when the wind increases in strength. They probably go to the shelter of the protecting hills on the other side of the creek (Fig. 1).

5. SUNSHINE DURATION AND BIRD VARIATIONS

A review of the literature on sunshine has already been made under climatic factors; so it is only necessary here to call attention to a few of the more important points. Rowan's data (1925, 1926, 1927) indicate that bird migration is related to hypertrophy and atrophy of the gonads and that this

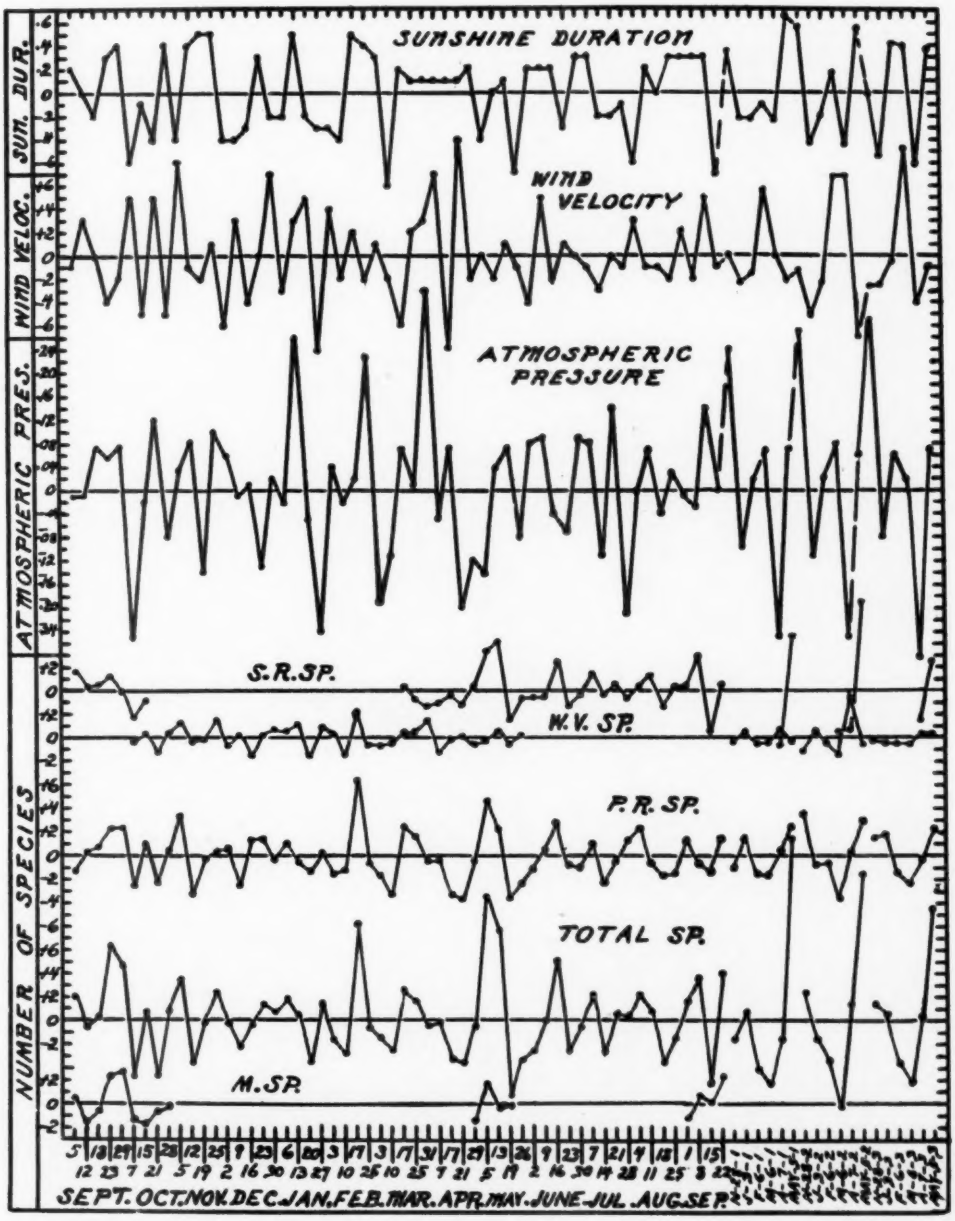

FIG. 24. The Relation between Certain Weather Factors (Wind Velocity, Sunshine Duration, and Atmospheric Pressure) and the Numbers of Bird Species Present on a Depositing Creek Bank. Legend as in Figure 7.

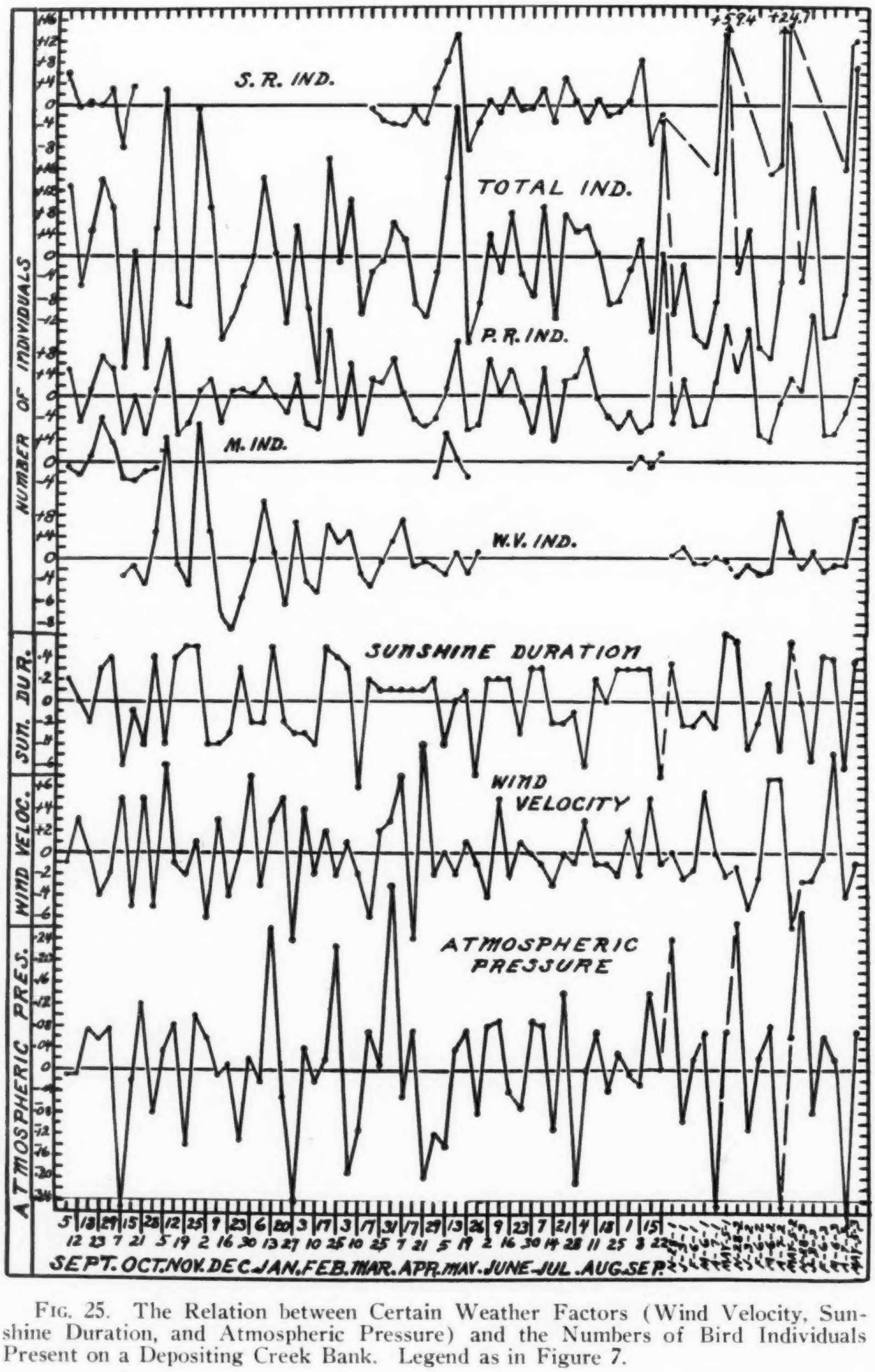

FIG. 25. The Relation between Certain Weather Factors (Wind Velocity, Sunshine Duration, and Atmospheric Pressure) and the Numbers of Bird Individuals Present on a Depositing Creek Bank. Legend as in Figure 7.

TABLE XVII. *The relation between wind velocity deviations and bird deviations.*

Bird Group	Weather Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Wind velocity deviations at hr. of study	—0.224±0.108	—0.150±0.111
P. R. Ind......	Wind velocity deviations at hr. of study	—0.261±0.106	—0.109±0.113
W. V. Ind......	Wind velocity deviations at hr. of study	—0.007±0.114	....
S. R. Ind......	Wind velocity deviations at hr. of study	....	—0.437±0.092

gonad relation is due to relative length of day to night. Haecker (1916, 1924) found that the time of beginning of the morning song and the time of ending of the evening song in relation to sunrise and sunset, respectively, was related to light. Shaver and Walker (1931) found similar relations to light in the case of the evening song of the southern robin and the eastern mockingbird. In the above cases, variations due to climatic sunshine were not separated from these due to weather sunshine, as has been done in the present study.

These studies indicate the very great importance of light to bird activities. Thus one might reasonably expect to find the birds on the depositing creek bank affected in their local movements by the degree of sunshine. However, a graphical comparison (Figs. 24 and 25) indicates no apparent relation. Similarly, the coefficients of correlation (Table XVIII) are low

TABLE XVIII. *Relation between sunshine duration deviations and bird deviations.*

Bird Group	Weather Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Sunshine duration deviations at hr. of study..........................	0.060±0.114	0.408±0.095
P. R. Ind......	Sunshine duration deviations at hr. of study..........................	—0.150±0.111	0.165±0.111
W. V. Ind......	Sunshine duration deviations at hr. of study..........................	—0.235±0.108	....
S. R. Ind......	Sunshine duration deviations at hr. of study..........................	....	0.520±0.083

with the exception of those for total individuals and summer resident individuals during the summer half year. Summer residents and total birds especially have a high correlation with sunshine. This is interpreted to mean that these birds come to the depositing creek bank on sunny days and leave it on cloudy ones. During the winter there is very little correlation between birds and sunshine. Winter visitants even have a negative correlation.

6. Atmospheric Pressure and Birds

A graphical comparison of atmospheric pressure fluctuations and the fluctuations of bird numbers on the depositing creek bank was first made (Figs. 24 and 25). From these figures, there appeared to be no relation. Coefficients of correlation (Table XIX) were also low.

TABLE XIX. *Relation between atmospheric pressure deviations and bird deviations.*

Bird Group	Weather Factor	Correlation coefficients for September 21—March 21	Correlation coefficients for March 21—September 21
Total Ind......	Atmospheric pressure deviations at hr. of study........................	—0.051±0.114	0.216±0.109
P. R. Ind......	Atmospheric pressure deviations at hr. of study........................	—0.083±0.113	0.259±0.106
W. V. Ind......	Atmospheric pressure deviations at hr. of study........................	0.069±0.113	....
S. R. Ind......	Atmospheric pressure deviations at hr. of study........................	....	0.317±0.103

In general then there appears no relation between the daily fluctuations of atmospheric pressure and that of birds during the fall and winter season and only relatively small correlations in the spring and summer. These latter with total individuals and summer residents may be large enough to be significant but it is somewhat doubtful in view of their high probable errors.

7. Summary and Discussion of the Effect of Weather on Bird Numbers

(1) There is very little relation between weather and the numbers of birds on the depositing creek bank.

(2) The correlations between weather factors and the fluctuations of bird numbers here during the spring and summer season appear to rank in this order: (a) sunshine duration; (b) relative humidity; (c) atmospheric pressure; (d) wind velocity; (e) temperature.

(3) During the fall and winter season the correlations are very small, the two highest being with sunshine duration and with wind velocity.

(4) The most conservative groups are permanent residents and winter visitants.

(5) The highest correlation (.520 ± .083) is between summer residents and sunshine duration.

(6) This analysis has apparently not thrown much light upon the relation between bird numbers and weather phenomena in a particular habitat—the depositing creek bank—because of the smallness of the correlations. Yet it is possible that all of these factors have some influence and no one stands out

markedly from the others. If this were true, the numbers of birds present would be correlated with some combination of all the weather factors.

The basis for making combinations, such as those mentioned, must be derived from controlled laboratory experimentation. Data similar to that accumulated by Shelford (1927) for the codling moth is needed for the warm-blooded animals. It is hoped that experiments of this kind on birds may soon be undertaken.

VIII. SUMMARY AND CONCLUSIONS

(1) Data on the numbers and kinds of birds present on a depositing creek bank were collected under the climate and weather conditions of Nashville, Tennessee, during 1922, 1923, 1925, and 1926.

(2) The field work involved seventy-four trips distributed over seventy-four weeks.

(3) The field data on birds were classified under permanent residents, winter visitants, summer residents, migrants, and total birds. Each of these groups was carefully smoothed so as to get the slow seasonal rhythm unmodified by daily fluctuations.

(4) The normal values of seven climatic factors were secured from the Nashville Weather Bureau, namely, temperature, relative humidity, precipitation, wind velocity, wind direction, sunshine duration, and atmospheric pressure. In addition, the values of each of these (except wind direction) for the actual hours of the field studies were carefully smoothed. These smoothed values closely approached the normal or climatic values.

(5) The curves of bird abundance were compared with these normal climatic curves in a general way. The most valuable results came however from correlating the smoothed curves of weather factors (representing climate) with the smoothed curves of bird abundance. Many of the correlation coefficients were quite high and significant. For all groups of birds, the coefficients of correlation ranked in this order: (a) temperature; (b) sunshine duration (the correlation was plus in the fall and winter season and minus in spring and summer); (c) relative humidity (the correlation was minus in fall and winter and plus in spring and summer—the reverse of sunshine duration); (d) wind velocity; (e) atmospheric pressure; and (f) precipitation.

(6) The deviations from the smoothed curves of bird abundance were assumed to be due to conditions that fluctuated from day to day. Apparently the most important fluctuating conditions are those of weather factors. These last factors were derived by getting the deviations of temperature, relative humidity, sunshine duration, wind velocity and atmospheric pressure from their smoothed values.

(7) Correlations between deviations in bird abundance and weather deviations were calculated. For the most part these correlations were very

low with rather high probable errors and hence cannot be regarded as of the same significance as are many of the correlations with climatic factors. As with climate, permanent residents and winter visitants are the most conservative. Summer residents show the highest correlations in the following order: (a) sunshine duration; (b) relative humidity (a minus correlation); (c) atmospheric pressure; (d) wind velocity; and (e) temperature.

In conclusion, it is a pleasant duty to acknowledge some of the writer's outstanding obligations. Especial thanks are due Dr. W. C. Allee for helpful advice and criticism during the progress of this work, to the General Education Board and to Dr. Bruce R. Payne for financial assistance, and to the Nashville Weather Bureau for kindly furnishing climatic and weather data.

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